Lagrangian analysis of sea turtle ecology.

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LAGRANGIAN ANALYSIS OF SEA TURTLE ECOLOGY

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(BSc Ecology; MSc Biodiversity Conservation)

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Abstract

Many marine organisms are highly mobile, which presents a variety of research and conservation management challenges. Sea turtles are a particularly paradigmatic group of long distant migrants whose movements as adults have been detailed by satellite tracking technology. However, small hatchlings are not amenable to this approach. This thesis used Lagrangian oceanography approaches to study the cryptic lives of juvenile turtles, since ocean currents drive their dispersion from natal beaches. Through increasingly sophisticated and novel uses of Lagrangian surface drifter buoys, state-of-the-art global ocean models and emerging animal life history datasets, my PhD thesis details significant findings of the key life history attributes of these enigmatic migrants. Initially, I modelled the dispersal of hatchlings from their nesting beaches to derive the first robust estimates of hatchling growth rates and by so doing, highlighted the long maturation times of turtle species. Then, I programmed hatchling swimming behaviour into ocean model simulations to reveal how these small drifters could improve their survival chances in strong current flows. More interdisciplinary research also highlighted aberrant routes of dispersal that can arise through storm displacements. Subsequent meta-analysis on the movements of flying, swimming and walking migrants highlighted key biological determinants of sea turtle migrations. Spatio-temporal analysis of sea turtle marine protected area (MPA) use highlighted minor (tractable) legislative revisions that would significantly improve MPA effectiveness. Finally, research culminated in a global synthesis of the movement patterns of adult and hatchling sea turtles which provided global support for a new migration paradigm, that whilst adult turtles travel independently of ocean currents, ocean currents still indirectly drive the ontogeny of adult sea turtle migrations and foraging habitat selections due to their past experiences as drifting hatchlings. This new understanding into the biological and physical determinants of sea turtle migration strategies is thus hoped to have broad conservation utility.

Contents

Chapters

Acknowledgements

I would like to thank everyone that supported me throughout my PhD; in particular my parents Sonya and Tony. After I first saw sea turtles whilst on a family holiday in 2004, I instantly became fascinated by their life histories and knew that I wanted to study these amazing creatures. Now that I have achieved this dream, I hope that I have made my parents (and everyone else) proud, particularly since my PhD ended up coinciding with three incredibly difficult years. In the first month of starting my PhD I became ill and was rendered either "out of action" or unable to work to my full potential for the first year. In the second year of my PhD my world fell apart after my dear friend Joana Yeates was murdered. I am therefore very grateful for the support and patience of all my friends, family and my supervisor's Graeme Hays, Robert Marsh and Rory Wilson during periods of ill health and bereavement.

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Introduction and overview

The status of marine ecosystems is now a major global concern due to the increasing array, and intensity, of anthropogenic pressures placed on these systems (e.g. Jackson *et al.* 2001; Halpern *et al.* 2008). One of the most direct and pervasive threats facing marine ecosystems, is the overexploitation of large marine vertebrates such as sea turtles (Pauly *et al.* 1998; Pauly and Watson 2005), due to the important roles these large consumers play in maintaining the structure and functioning of their foraging habitats (Jackson *et al.* 2001; Pandolfi *et al.* 2003). Many sea turtle populations have been subjected to high levels of past direct exploitation and all populations face multiple pressures from other indirect threats/exploitation such as pollution and fisheries by-catch (Jackson *et al.* 2001). The life cycles of sea turtles typically involve various ontogenetic habitat shifts, long distance breeding migrations and an oceanic juvenile dispersal phase. These life history attributes thus render sea turtle populations notoriously difficult to study/conserve, and all species are now of conservation concern (IUCN 2012). Given the increasing concerns over many marine populations and ecosystems there is now an urgent need for ever innovative approaches to guide research and conservation efforts.

Once such innovation arose through the advent of high frequency radio technology in the 1970s and the subsequent development of satellite telemetry devices. These devices were first used to track the movements of large marine species in the 1980s, and since the 1990's deployments of increasingly sophisticated biotelemetry devices on species such as sea turtles, has risen exponentially (Godley *et al.* 2008). Through the Argos satellite-based platform (http://www.argos-system.org/), this technology has proved instrumental in detailing previously cryptic life history aspects such as the post-breeding migrations of adult sea turtles to their foraging habitats (e.g. Papi *et al.* 2000; Broderick *et al.* 2007) and more recently, the movements of large juvenile turtles (e.g. Mansfield *et al.* 2009; Hart and Fujisaki 2010). Nonetheless, whilst fiscally dictated sample sizes within many satellite tracking projects can constrain the conservation impact of these data, emerging biotelemetry datasets have paved the way for recent global syntheses of sea turtle life histories (Godley *et al.* 2008; Hamann *et al.* 2010). Prior to starting my PhD, I studied for an MSc in Biodiversity Conservation at the University of Exeter in Cornwall. Supervised by Professor Brendan Godley, I conducted the first quantitative

global synthesis that combined sea turtle biotelemetry and environmental datasets (Scott *et al.* 2012). Global synthesis of this nature can enable a number of key ecological questions which can feed into spatially relevant management to be addressed, and my MSc degree confirmed my desires to continue conducting research in this area.

Whilst a wealth of qualitative satellite tracking data on the movements of adult turtles is in now available, one of the biggest biotelemetry challenges is the miniaturisation of satellite tracking devices. Consequently, hatchling sea turtles are too small to be tracked in this way, and the juvenile life stage remains the least understood aspect of sea turtle life histories. For most species and populations even the location and duration of juvenile stage is unknown and hence this period is still commonly referred to as the "lost years" (after Carr 1986) as hatchlings effectively disappear into the ocean after they emerge from their nests (e.g. Carr 1986; Bolten *et al.* 2003). Initial knowledge of the juvenile life stage arose primarily through captive studies of hatchlings. For example, these studies have revealed that hatchlings embark on an initial "swimming frenzy period" fuelled by egg yolk reserves (Kraemer and Bennett, 1981; Salmon and Wyneken 1987). This hyperactive period of offshore swimming lasts several days (Salmon and Wyneken 1987) and is presumed to help post-hatchlings reach offshore currents that transport them away from predator rich coastal waters to safer oceanic development habitats. Juvenile turtles are then typically not seen again until they are much larger, and start to recruit back to neritic foraging grounds closer to their natal beaches (Carr *et al.* 1987; Sears *et al.* 1995). Here, they complete their development to maturity, then return to their natal area to breed as neophytes before embarking on regular (typically every $\geq$ 2 years) breeding migrations between their natal nesting beaches and adult foraging habitats (Hughes *et al.* 1995). Molecular evidence and repeated satellite tag deployments on individuals have shown that adult hard-shelled turtles (family Chelonioidea) can show very high fidelity to their natal nesting and coastal foraging sites which are typically several hundreds to thousands of kilometres apart (e.g. Broderick *et al.* 2007; Godley *et al.* 2008; Lee *et al.* 2007). Whilst the six species of hard-shelled turtles typically forage in discrete costal habitats (see Godley *et al.* 2008), the leatherback turtle (*Dermochelys coriacea*) is the only species of soft-shelled turtle (family Dermochelyidae). Unlike most hard-shelled turtles, leatherback turtles forage pelagically, whilst travelling, and can perform transoceanic wandering movements in the process (e.g. Fossette *et al.* 2010).

It was first hypothesised that hatchlings may also embark on transoceanic journeys, (albeit, through passive transport with ocean currents) based on their small size, weak swimming abilities and initial observations of small juvenile loggerhead turtles living/feeding in association with drifting Sargassum communities in the North Atlantic gyre (e.g. Smith 1968; Carr 1987). Carr (1987) also highlighted that the size of turtles encountered in the Eastern Atlantic (principally around the Azores and Madeira) represented the "missing size class" of turtles between hatchling and recruiting back to Western Atlantic coastal habitats as larger juveniles. Since the first speculative evidence of juvenile transoceanic dispersal, it is now well documented for other sea turtle species, and populations. Due to natal philopatry (adults return to where they were born to breed), and the resultant genetic isolation among nesting populations, population specific genetic markers are now routinely used to assign juvenile turtles captured at their feeding grounds to their respective rookery of origin (e.g. Bowen and Karl 2007). For example, genetic studies confirmed that juvenile turtles encountered around the Azores and Madeira, originated from Western Atlantic nesting populations (Bolten *et al.* 1998). This technique also revealed that post-hatchling loggerhead turtles embark on transoceanic journeys in the North Pacific Gyre, to juvenile feeding grounds c.10,000 km away (Bowen *et al.* 1995) and more recently, that juvenile green and hawksbill turtles can also embark on journeys of this magnitude (Monzón-Argüello *et al.* 2010; Monzón-Argüello *et al.* 2011). Basic knowledge of ocean currents has been used to support these studies in terms of detailing the potential dispersal routes between distant foraging and genetically assigned natal nesting sites (e.g. Monzón-Argüello *et al.* 2010). Whilst it is now well established that small post-hatchling turtles are dispersed with (and indeed reliant on) ocean currents to reach their development habitats (Witherington 2002), they may also undertake in short periods of directed swimming to help facilitate dispersal (e.g. Lohmann *et al.* 2001).

Whilst hatchlings cannot be directly tagged/followed on these long journeys, Lagrangian oceanography approaches have great application for studying the cryptic dispersion of hatchlings during the "lost years". There are two approaches to measuring ocean currents: Eulerian and Lagrangian. Eulerian measurements record ocean current properties (speed, direction etc) that flow past a specified recording station. Lagrangian measurements are made by following the movement trajectory of an object (e.g. a

satellite tracked buoy) or a parcel of water (e.g. with coloured dye). Since 1979 over 15,600 satellite tracked Lagrangian surface drifter buoys have been deployed in the world's oceans as part of the Global Drifter Programme (GDP). The GDP is a branch of NOAA's (National Oceanic and Atmospheric Administration) Global Ocean Observing System (GOOS) and a scientific project of the Data Buoy Cooperation Panel (DBCP). Data from the GDP is available online (http://www.aoml.noaa.gov/phod/dac/index.php) and managed by NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML) and NOAA's Joint Institute for Marine Observations (JIMO). Satellite tracking technology has thus also had great application in the field of oceanography as well as animal movement ecology. This freely available dataset presents a very accessible tool for marine biologists to assess the impacts of ocean currents on marine organisms. However, restricted spatial and temporal coverage of buoys can limit the utility of this dataset since coverage typically reflects infrequent batch deployments from targeted research cruises or ships of opportunity (Lumpkin and Pazos 2006).

A second recent major innovation in Lagrangian oceanography occurred with the development of high resolution global ocean general circulation models. These models mathematically describe currents flows by forcing the ocean surface with wind data and buoyancy fluxes (heat and freshwater exchange). When models are used with particle tracking software the Lagrangian trajectories of simulated particles (representing virtual parcels of water as they drift in modelled ocean current simulations) can be tracked and physical oceanographers have used this approach to study large scale ocean circulation for several years (e.g. Döös, 1995; Blanke and Raynaud, 1997; Blanke *et al.* 2001 Marsh and Megann 2002). Recent advances in computational power, coupled with more sophisticated/accurate numerical model equations and oceanographic data used to force the models has greatly improved the spatio-temporal resolution of models and thus their application for marine biologists (Fossette *et al.* 2012). Consequently, by capitalising on these recent advancements, Lagrangian oceanography approaches can be used in innovative ways by biologists interested in the pathways that passively drifting organisms will follow. For example, virtual particles released offshore from sea turtle nesting rookeries and tracked in a Lagrangian framework were first used to represent passively drifting "virtual hatchling turtles" during the cryptic "lost years" by Hays and Marsh (1997). Furthermore, modelled particle and surface Lagragian drifter buoys trajectories nicely complement each other since buoys provide empirical in-situ

measurements which can be used to verify *in-silico* modelled Lagrangian trajectories, and *in-silico* approaches are less restricted in their spatial/temporal coverage than drifter buoys.

In the last few decades, our understanding of aspects of sea turtle life histories has increased greatly through emerging datasets (e.g. from satellite telemetry, genetics, and fisheries by-catch studies). Furthermore, the field of oceanography has rapidly advanced in recent years with the global surface drifter buoy array and state-of-the-art high resolution global ocean circulation models. It was thus timely for a PhD that capitalised of these important developments and existing datasets. Consequently, the first 4 chapters of my PhD were based on novel interdisciplinary research and the collaboration with other biologists, oceanographers and geneticists to further understanding of the juvenile dispersal phase. These chapters focused on loggerhead turtles in the North Atlantic since the best existing datasets on hatchlings (from which my work could build upon) were available in this region. For the next chapter of my PhD, I performed global meta-analysis of the migratory distances travelled by turtles and other flying, marine and terrestrial migrants. For the penultimate chapter of my PhD, I collaborated on a project where I conducted analysis into the effectiveness of MPA legislation for protecting a population of loggerhead turtles. The final, and by far the most substantial chapter of my PhD, was a global meta-analysis of the post-breeding migrations of satellite tracked adult sea turtles and Lagrangian analysis of hatchling dispersion from these breeding grounds which provided compelling support for a new paradigm on the ontogeny of sea turtle migrations. The following paragraphs of this introduction further detail the reasoning and chronology behind each of these chapters along with a summary of the main findings. Throughout this thesis, any abbreviations and specialist terminology are defined at first use.

CHAPTER 1: Scott, R. Marsh, R. and Hays, G.C. (2012) Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles. *Functional Ecology*, **26**, 227-235.

My PhD supervisors Graeme Hays and Robert Marsh were the first to utilise Lagrangian drifter buoys and a 1° resolution ocean model (then state-of-the-art) to provide the one of the first estimates of a key life history attribute; the growth rates of

wild post-hatchling loggerhead turtles (Hays and Marsh 1997). This novel approach was based on (1) the size of neonate hatchlings emerging from nests in the south east USA, (2) the size of post-hatchlings that stranded in Northern Europe (and likely drifted here from sea turtle nesting rookeries in the SE USA) and (3) Lagrangian derived drift times between these locations from ocean model particle simulations and five surface drifter buoys that completed this journey. Since this publication, datasets on the size of post-hatchlings encountered at foraging sites in the North Atlantic and North Pacific and from subsequent drifter buoy deployments have grown considerably. Hence, the first chapter of PhD set out to revise and expand upon this initial study. Through the global surface drifter buoy database alone, over 500, 1000 and 6000 drift times could now be calculated from SE USA rookeries to stranding destinations in Northern Europe, from SE USA rookeries to juvenile foraging habitats around the Azores and from rookeries in Japan to juvenile foraging habitats in the central North Pacific (respectively). Since post-hatchlings drifting to the cold waters of Northern Europe had died prior to stranding from cold stunning, we used newly available information on the size of post-hatchlings that arrived at favourable (and warm) juvenile oceanic foraging habitats around the Azores, to produce the first robust estimate of hatchling growth rates in the North Atlantic. Growth rates estimates were also calculated in the same way for hatchlings originating in Japan that drifted to oceanic foraging habitats in the North Pacific Gyre. When analysed in conjunction with direct measurements of the growth rates of adult and sub-adult turtles at more accessible coastal nesting and foraging locations (amenable to mark, recapture measurement studies), we produced the most robust loggerhead turtle growth curve and age at maturity estimate to date. Furthermore, by using our new age at maturity estimate of 45 years within a meta-analysis of the age at maturity of other reptile species, we highlight important conservation implications that the time taken for turtle and tortoise species to reach maturity is much longer than other large-bodied reptile species.

CHAPTER 2: Scott, R., Marsh, R. and Hays, G.C. (2012) A little movement oriented to the geomagnetic field makes a big difference in strong flows. *Marine Biology*, **159**, 481-488.

Whilst the dispersal of post-hatchlings is driven by passive drift with surface ocean currents, laboratory experiments have shown that they may embark on periods of active

directional swimming (e.g. during the swimming frenzy) which is believed to help them reach favourable development habitats (Salmon and Wyneken 1987). In the North Atlantic, loggerhead turtle hatchlings from major nesting rookeries in the SE USA risk being transported along death trajectories with the North Atlantic current out of the warm North Atlantic gyre towards Northern Europe. Elegant laboratory experiments have revealed that new-born hatchlings from the SE USA altered their swimming direction in response to different inclination and intensity signatures of the Earth's magnetic field present at different locations in the North Atlantic Gyre (Lohmann *et al.* 2001; Putman *et al.* 2011). Broadly speaking, hatchlings tended to adopt swimming directions orientated towards the centre of the North Atlantic gyre and hence the use of geomagnetic information as a navigational signpost was proposed to aid post-hatchling entrainment in favourable warm development habitats within the gyre. Nonetheless, it remained equivocal as to whether a small post-hatchling could actually alter its destiny with relatively limited amounts of directional swimming in strong current flows. The second chapter of my PhD thus set out to investigate this. To do this, I programmed empirical data from the aforementioned laboratory experiments on the geomagnetic directional swimming behaviour of hatchlings into particle trajectories from a high-resolution (1/4°) global general circulation ocean model. The eddy resolving ocean model used was based on a version of NEMO (Nucleus for European Modelling of the Ocean; Madec 2008) developed at the National Oceanography Centre in Southampton. This model resolves the mesoscale variability of energetic currents, such as the Gulf Stream providing a major advance over an earlier study of hatchling dispersal in this region based on the coarser model available at the time (Hays and Marsh 1997). In so doing, we revealed for the first time that whilst ocean currents drive the dispersal trajectories of hatchlings, a small amount of directional swimming was significantly advantageous for hatchlings and helped them to remain in safer, warmer current flows (away from Northern Europe) where survival and fitness potential is higher. Since the Gulf Stream is one of the world's strongest ocean current flows and swim speeds of the larval stages of other marine species (e.g. fish) can be considerably higher than those of loggerhead hatchlings (Fisher 2005), the coupling of accurate parameterisation of organism swimming behaviour into high-resolution ocean general circulation models is hoped to have significant application in the management of a range of species of conservation concern.

CHAPTER 3: Putman, N.F., **Scott, R.,** Verley, P., Marsh, R. and Hays, G.C. (2012) Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles. *Marine Biology*, **159,** 2117-2126.

During the second year of my PhD, I attended the international Royal Institute of Navigation (2011) conference in Reading. Here I met Nathan Putman, a PhD student (at the time) working with Ken Lohmann. Nathan was collaborating with the oceanographer Phillipe Verley and also conducting research on the dispersal of loggerhead turtles from the SE USA, using a 0.08° resolution Global HYCOM model (Global Hybrid Coordinate Ocean Model; Bleck, 2002). Nathan had recently published a paper which revealed that loggerhead turtle nesting densities around the coast of the SE USA (from Texas to North Carolina), were negatively correlated with the distance between the coast and the Gulf Stream (Putman *et al.* 2010). Since hatchlings are reliant on offshore currents such as the Gulf Stream, for dispersal away from predator rich coastal waters, proximity to the Gulf Stream can be expected to influence hatchling survival and thus adult nesting densities due to natal philopatry. In light of our research interests, a collaboration arose to (1) assess hatchling dispersal and predicted survival scenarios at these different nesting regions (from Texas to North Carolina) and (2) assess the impact of the hatchling swimming frenzy on hatchlings survival by programming swimming frenzy behaviour into model simulations. Drift scenarios were computed using both the NEMO and HYCOM ocean models and surface drifter buoy data. Reassuringly the same conclusions could be drawn from the two ocean models and drifter buoys; that surface currents differed between nesting regions in how well they facilitated offshore dispersal past oceanic fronts (which retain passive drifters in coastal waters). Furthermore, adding swimming frenzy behaviour into simulations revealed that even a small amount of offshore swimming during the week long frenzy period significantly facilitated offshore dispersal and improved the survival chances of hatchlings. This was most notable for regions, typically those closest to the Gulf Stream, where passive transport was most favourable. These results have broad implications for understanding the potential movement processes (in terms of offshore dispersal versus coastal retention) for a range of planktonic and more nektonic species.

CHAPTER 4: Monzón-Argüello, C., Dell'Amico, F., Morinière, P., Marco, A., López-Jurado, L.F., Hays, G.C., **Scott, R.,** Marsh, R. and Lee P.L.M. (2012). Lost at sea:

genetic, oceanographic and meteorological evidence for storm-forced dispersal. *Journal of the Royal Society Interface,* **73**, 1725-1732.

A second collaboration arose when Caty Monzón-Argüello started a post-doc position at Swansea University. Caty's PhD had focussed on the genetic structure and connectivity of sea turtles in the Eastern Atlantic and whilst in Swansea, she was conducting genetic research with Dr Pat Lee on juvenile loggerhead turtles that had stranded in the Bay of Biscay. Genetic analysis of these turtles revealed that the majority had originated from SE USA nesting rookeries. This was to be expected given the prevailing currents in the North Atlantic. A high proportion of turtles also originated from the Eastern Atlantic Cape Verde Islands and it was very noteworthy that (1) 84% of these Cape Verde turtles were dead compared to just 29% of the turtles that stranded from the SE USA and (2) the stranding occurrences of Cape Verde turtles were much more irregular than American turtles. In light of these interesting findings, which were discussed between Caty, Pat and Graeme, I was asked to use Lagrangian oceanography approaches to assess the physical oceanography and thus potential connectivity between the Bay of Biscay and Cape Verde Islands. My contribution towards this paper revealed that dispersal with prevailing ocean currents between these sites could not explain how these small juveniles arrived in the Bay of Biscay from Cape Verde. Realising that something else must have caused these interesting findings, Caty looked at storm data and found that a number of large storms passed near to the Cape Verde Islands during the hatchling season and headed North during the periods that Cape Verde turtles stranded in the Bay of Biscay. Hence, whilst these juveniles did not arrive in the Bay of Biscay through dispersion with surface ocean currents, storms trajectories would have provided a far more direct (and quicker) route that explained the higher mortality rates and irregular stranding occurrences of Cape Verde turtles. Hence, by combining genetic, oceanographic and atmospheric data, we show that whilst prevailing oceanographic forces are the primary determinant in the dispersal of drifting organisms, storms can displace organisms along aberrant routes. Storm displacements may thus lead to novel dispersal or migration patterns, if hatchlings survive and are displaced to favorable habitats. With climate change predicted to alter the trajectories and frequency of storms, storm driven displacements will play an increasingly important role in the dispersal of surface marine organisms.

CHAPTER 5: Hays, G.C. and **Scott, R.** Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals, *Functional Ecology,* in press.

With the wealth of data now available on the movements of adult and juvenile turtles from satellite tracking and genetic studies, it was timely to conduct a global meta-analysis on the distances that sea turtles migrate. Synthesis of data from 407 post-nesting adult turtles tracked to their foraging habitats and 4715 juvenile turtles captured at their foraging grounds and genetically assigned to natal nesting rookeries revealed: (1) the maximum migration distances travelled by adult hard shelled (cheloniid) turtles were performed by green turtles migrating c.2850 km from Ascension Island to Brazil (Papi *et al.* 2000; Hays *et al.* 2002) and (2) that adult leatherback turtles and juvenile hard shelled turtles routinely foraged in habitats > 10,000 km from their natal breeding areas (e.g. Boyle *et al.* 2009; Benson *et al.* 2011). Unlike leatherback turtles and juvenile turtles, adult cheloniid turtles tend to fast whilst away from their foraging habitats. For adult cheloniid turtles, theoretical calculations conducted by Graeme Hays suggested that the observed upper ceiling in migration distance (c. 2,850 km) is close to the predicted physiological maximum distance (imposed by fuel stores) that a turtle which fasts can travel. Leatherback turtles and juvenile turtles are freed of this upper ceiling on migration distance because they do not fast while travelling between their breeding and feeding grounds. Furthermore, juvenile turtles only make one return migration from their development habitats back to their natal area and hence can forage much further from their natal sites than adults on their regular breeding migrations. At the time of these findings, a paper had just been published by Hein *et al.* (2012) which compared maximum migration distances of walking, swimming and flying migrants. The work of Hein *et al.* (2012) highlighted that migration distances increase with species body mass, albeit with different relationships among flyers, swimmers and walkers. Since the study by Hein *et al.* (2012) did not include sea turtles, I was keen to build upon our findings and those of Hein *et al.* (2012) to establish where the upper ceiling on migration distance in sea turtles lay compared to other migrants. In so doing, we showed that the maximum migration distances of adult turtles were comparable (within the 95% predictive intervals) of equivalent sized swimming fish and marine mammals. However, the maximum migration distance for juvenile sea turtles was significantly greater than that predicted for equivalent sized swimmers, and more akin

to the migrations performed by similar sized birds. Our results thus highlighted the important roles migration periodicity and foraging mode can play on shaping species migrations.

CHAPTER 6: Schofield, G., **Scott, R.,** Dimadi, A., Fossette, S., Katselidis, K.A., Koutsoubas, D., Lilley, M.K.S., Pantis, J.D., Karagouni, A.D., Hays, G.C. Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate. (in review; *Biological Conservation*).

During the final year of my PhD I was delighted to get the opportunity to spend two weeks helping to deploy satellite tags on loggerhead turtles in the National Marine Park of Zakynthos. Since one of the main limitations of many satellite tracking projects are fiscally dictated sample sizes, it was great to have been involved with this project where > 100 biotelemetry devices have now been equipped on turtles. Whilst it was a fantastic opportunity to learn new field skills, my time in Greece also lead to a collaboration on a study lead by Gail Schofield which formed the penultimate Chapter of my PhD thesis. In this study, I was responsible for conducting all the spatial analysis of satellite tracking data to investigate the spatio-temporal habitat use of turtles within the National Marine Park of Zakynthos. My spatial analysis revealed two main findings: (1) the main area used by both male and female turtles were concentrated in a small core area, and (2) turtles migrated into the MPA several months before existing seasonal legislation designed to protect the turtles is enforced. By conducting a detailed assessment into the effectiveness of the current MPA legislation for sea turtle protection, it is hoped minor proposed adjustments to the existing legislation will be implemented to maximize sea turtle protection whilst minimizing negative impacts on other stakeholders.

CHAPTER 7: Scott, R., Marsh, R., and Hays, G.C. Ontogeny of a new migration paradigm: Global Lagrangian support that ocean currents drive sea turtle migratory strategies.

Shortly after starting my PhD, Graeme Hays published a study where a novel migration paradigm was proposed; that ocean currents may drive the migrations and foraging site selections of adult sea turtles. Whilst adult turtles do not drift with ocean currents, Hays *et al.* (2010) hypothesised that their movements may be shaped by ocean currents

through an indirect mechanism; whereby adult turtles return to sites that they had previously encountered as passively drifting hatchlings. This new migration paradigm emerged because the north/south dichotomy in the post-breeding migrations of satellite tracked loggerhead turtles from Zakynthos, were hypothesised to reflect hatchling drift pathways (detailed by surface drifter buoys and ocean model simulations) arising from a strong north/south dichotomy in ocean current flows at this nesting site. The final chapter of my PhD thus set out to test this hypothesis on a global scale, by conducting a global meta-analysis of the post breeding migrations of satellite tracked adult sea turtles combined with Lagrangian analysis of hatchling dispersion (based on the pathways of 42,000 *in silico* and c. 2000 in situ ocean drifters). In so doing, global support was provided that ocean currents drive the ontogeny of different sea turtle migration strategies through two main mechanisms. Firstly, as proposed by Hays *et al.* (2010), most adults turtles returned to sites they would have encountered as hatchlings (albeit, typically along a more direct route than the often convoluted routes of drifting hatchlings). Secondly, for some cheloniid turtle populations, the nearest potential adult foraging sites that hatchlings drifted to were too far away (> 4000 km) from their natal area for adult turtles to return on their regular breeding migrations. Hence at these sites, adult turtles became locally resident or foraged oceanically (if the breeding grounds were located on an island) or turtles performed coastal/shuttling migrations to fixed/seasonal habitats (if the breeding grounds were location on the mainland). Through this final chapter, significant advances have been made with regards to understanding the drivers that underpin the diverse range of sea turtle migrations strategies and foraging habitat selections. In addition to highlighting that the importance of studying hatchling dispersal extends beyond the direct implications for the early life history stages, to implications for turtles throughout adulthood, these findings are anticipated to have broad conservation applications.

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Chapter 1

Life in the really slow lane: loggerhead sea turtles mature late relative to other reptiles

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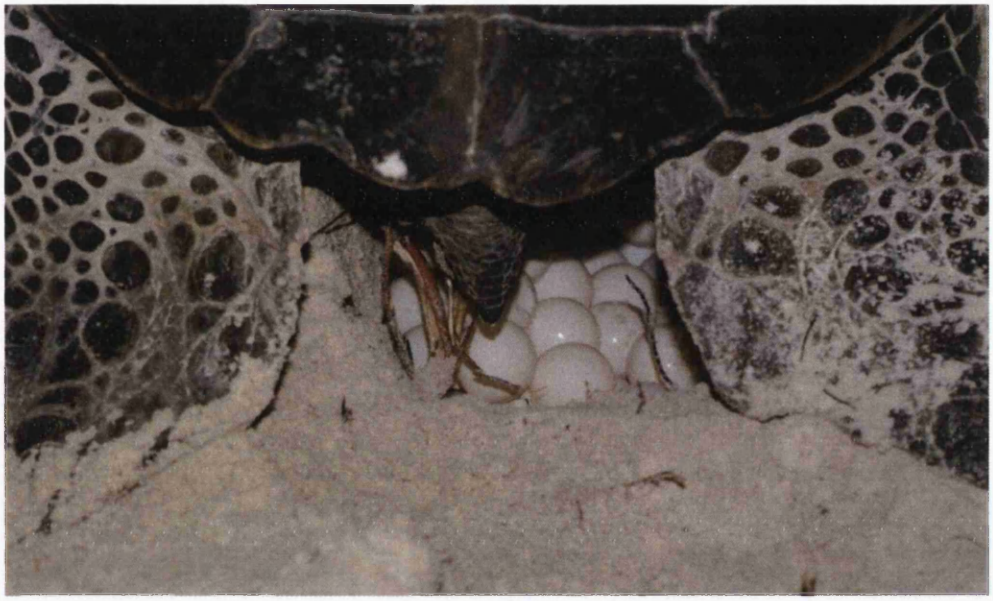

Disclaimer: RS complied and analysed all the datasets used in the study. GCH conceived the study. RM set up the ocean model so that RS could compute and analyse the ocean model trajectories. RS prepared all the figures and wrote the manuscript with GCH and RM.

Abstract

Age at maturity is hard to estimate for species which cannot be directly marked or observed throughout their lives and yet is a key demographic parameter that is needed to assess the conservation status of endangered species. For loggerhead turtles (*Caretta caretta*) in the North Atlantic and North Pacific, juvenile growth rates (c. 10 $cm.yr^{-1}$) were calculated by examining size increases during trans-oceanic journeys; durations of which were estimated from satellite tracked Lagrangian surface drifter buoy trajectories. Lagrangian derived growth estimates were used in a weighted log linear model of size-specific growth rates for loggerhead turtles and combined with newly available information on size at maturity to estimate an age at maturity of 45 years (older than past estimates). By examining the age at maturity for 79 reptile species, we show that loggerhead turtles, along with other large bodied Testudine (turtle and tortoise) species, take longer to reach maturity than other reptile species of comparable sizes. This finding heightens concern over the future sustainability of turtle populations. By maturing at an old age, sea turtles will be less resilient to anthropogenic mortality than previously suspected.

Introduction

Age at maturity has long been recognized as a fundamental life-history component integral to demographic models and hence assessments of the conservation status of species (Lewontin 1965; Berner and Blanckenhorn 2007). In general, traits such as age at maturity typically scale with body size and species exhibiting late age at maturity tend to show a number of k life-history characteristics such as low intrinsic rates of population increase (Saether and Bakke 2000; Cardillo *et al.* 2005; Nee *et al.* 2005; Depczynski and Bellwood 2006; Hard *et al.* 2008). For example, for northern right whales (*Eubalaena glacialis*) in the Atlantic, the late age at maturity contributes to low reproductive output and hence the premature death of even a few mature females (e.g. through ship collisions) may drive the population to extinction (Fujiwara and Caswell 2001). Obtaining accurate estimates of age at maturity is thus crucial for determining the potential susceptibility of species and populations to declines or extinctions and for effective conservation management.

While the age of maturity is easily determined for captive animals, such studies are limited in that they may not reflect the age at maturity for free-living individuals. A variety of approaches have thus been developed for estimating the age at maturity for free-living animals. For species that can be directly observed and identified throughout their lives (e.g. through photo-identification or tagging) it is possible to directly measure age at first breeding. When species cannot be tracked throughout their lives, it may be possible to estimate the age of individuals through a number of indirect ways. For example, developing fish can be aged based on growth rings in their otoliths which have been used to show how commercial harvesting of fish has driven down the age and size of first breeding (Trippel *et al.* 1995; Shackell *et al.* 2010). For other taxa such as mammals and reptiles, age can be estimated through skeletochronology using growth rings in structures such as teeth and bones (Amano *et al.* 2011). One of the limitations of this approach however is that these bony structures are susceptible to the loss of growth layers resulting in a tendency to underestimate age at maturity (Parham and Zug 1997). Other techniques include the analysis of length frequency distributions; however limitations include assumptions that length frequency modes (if evident) represent single age classes (Bjorndal *et al.* 2000). Consequently, as a result of limitations and the intrinsic uncertainties of indirect aging methods, age at maturity is still not well known for many species. This is particularly apparent for long lived and highly mobile

marine species such as sea turtles (Cheloniidae and Dermochelyidae families) because of their life histories and associated logistical constraints, which prevents reliable and routine age assessments.

Directly recording the age at first breeding of free-living sea turtles is almost impossible because of difficulties associated with marking hatchlings in any way that they can be recognised later in life. Whilst mark-recapture studies enable size-specific estimates of the growth rates of sea turtles at adult nesting and sub-adult coastal development habitats, the early pelagic life-history stage of post-hatchlings coupled with their small size and low survival probabilities have prevented any success with mark-recapture studies (Lutz and Musick 1997). Consequently, age at maturity in sea turtles has been estimated in a number of indirect ways (e.g. skeletochronology and length frequency analysis) which has contributed to the range of age at maturity estimates both between and within different loggerhead turtle populations. For example, estimates of the mean age at maturity for loggerhead sea turtles (*Caretta caretta*) in the western North Atlantic range from 6.5 years (Caldwell 1962) to 39 years (NMFS-SEFSC 2001). With the onset of better data and methods driving this upwards revision in age at maturity estimates, robustness of estimates are still hindered by the paucity of growth rate estimates for free living post-hatchlings (Metcalfe and Monaghan 2001; Roark *et al.* 2009).

To estimate post-hatchling growth rates we estimated the time taken for individuals to drift from start (nesting) locations to end (stranding locations and/or development habitats) and the difference between the sizes of individuals between these two locations. Drift times were estimated using Lagrangian drifter trajectories, i.e. satellite tracked drogues carried by the prevailing surface currents. We focused our analysis on loggerhead sea turtles in the North Atlantic and North Pacific because of the availability of Lagrangian drifter data and size records of individuals. We have previously advocated that in certain circumstances, it may be possible to use drift times of hatchling turtles from nesting beaches to known foraging sites to estimate growth (Hays and Marsh 1997), i.e. if hatchlings enter the water at size x and arrive elsewhere at size y after a time interval t, then their growth rate is simply (y-x)/t. With the advent of easily accessible global datasets for satellite tracked Lagrangian drifter buoys (see Fossette *et al.* 2010; Hays *et al.* 2010) coupled with better sea turtle datasets on size distribution at different locations, it should now be possible to calculate robust estimates

for post-hatchling growth rates. Here we conduct this analysis for loggerhead sea turtles in two ocean basins and revise estimates for the age at maturity. We then perform a meta-analysis of reptilian age at maturity estimates to examine whether our revised estimates for sea turtles fit within general patterns across taxa. Finally we discuss the conservation implications of our findings.

Methods

Estimating drift times

All analyses were conducted using ESRI ArcGIS™ version 9.2 and R version 2.10.1 software (R Development Core Team 2009). Lagrangian drifter data were downloaded from the NOAA-AOML website: (http://www.aoml.noaa.gov/envids/gld/) with no restrictions on date or drogue attachment imposed. This dataset spans from 1979 to present and contains quality controlled data of over 14,500 satellite tracked surface buoys (drogued at 15m to reduce wind effects) interpolated to provide fixes at 6 hour intervals (Lumpkin and Pazos 2006). Due to the proximity of the strong boundary currents to the major loggerhead rookeries in Florida and Japan (Gulf Stream and Kuroshio current, respectively) and the weak swimming ability of neonate turtles (Salmon and Wyneken 1987) only drifters passing within 50km from major rookeries on the SE coast of USA and Japan were used to best represent drift trajectories that would be encountered by post-swimming frenzy hatchlings. Drift times for buoys that passed within 50km of nesting beaches and reached within 50km of locations for which size data of small loggerhead turtles were available were then calculated.

As a result of the long distance between nesting and re-encounter locations (several 1000 km), very few buoys completed the entire drift. To estimate drift times between Florida-Northern Europe and Florida-Azores, we therefore split each journey into two legs. These legs were selected based on the routes buoys followed between the respective sites. For the Florida-Northern Europe journey, leg one ended in an area off Nova Scotia (delineated by longitudes: 55° W to 45° W and latitudes: 45° N, to 35° N). For the Florida-Azores journey leg one ended when buoys reached a longitude of 55° W (Fig. 1a). In the North Pacific, the first leg of the journey was defined when buoys first reached the oceanic area (delineated by longitudes: 166° E to 170° W and latitudes: 45° N, to 28° N) where turtle size data were available. Due to the time buoys spent entrained in eddies in this general area, the second leg of the journey was defined as the

time buoys spent in this area before continuing along trajectories in the North Pacific gyre (Fig. 1b).

The impacts of any potential active directional swimming by post-hatchlings on drift times were estimated by placing realistic swimming behaviours (parameterised from laboratory experiments; Salmon and Wyneken 1987; Witherington 1991; Lohmann *et al.* 2001) using R software into passive particle trajectories from the surface current fields of a state-of-the-art ocean model hindcast. Passive particle trajectories were generated from particle releases from the SE USA using ARIANE software from an ocean model with $1/4^{o}$ horizontal resolution based on the Nucleus for European Modeling of the Ocean (NEMO) (see detailed supporting methodology in Appendix 1).

Size of loggerhead turtles

Information on the size and locations of small turtles in the North Atlantic and North Pacific were determined from a variety of fishing records and stranding reports (see Table S1 in Appendix 1). In the North Atlantic, we compared the size of neonate hatchlings reported at major rookeries in Florida (Dodd 1988) with the size of post-hatchlings recorded around the Azores and in northern Europe (around the UK and France). In the Pacific, we compared the size of loggerhead hatchlings (Dodd 1988), with the size of post-hatchlings reported in the central North Pacific. Different criteria were used to define the size of small turtles at arrival due to data availability and biological considerations associated with the different sites (further discussed in the results).

Growth/age at size curves

A comprehensive meta-analysis of size-specific loggerhead turtle growth rates was undertaken (see Table S2 in Appendix 1). Only direct measures of growth from marked and re-captured turtles were used to revise parameterisation of loggerhead turtle growth curves. To assign body size to reported growth increments, we took arithmetic means of marked and recaptured carapace lengths and straight carapace lengths (SCL) were converted to curved carapace lengths (CCL) (Witherington 2002). Data from marked individuals were only included when intervals between marking and recapture were known to be $\geq$365 days and $\leq$1460 days. When mean growth rates were reported for size

classes of marked individuals, only mean values based on individuals with recapture intervals ≥365 days were included in analyses.

Mark-recapture intervals were controlled for time, as short intervals (days/months) fail to account for seasonality of growth and amplify human measurement error (Chaloupka and Musick 1997), while large recapture intervals/growth increments are not an accurate measure of size-specific growth as growth rates decline non-linearly with increasing body size (Karkach 2006). Data availability dictated that our focal area for all subsequent analysis became the North Atlantic. Our post-hatchling growth rate estimate from the Azores was used to parameterise our growth curve because the growth rates of turtles stranding in Northern Europe are compromised due to cold stunning. By using direct measurements of size-specific growth supplemented with our size-specific growth rate estimate for post-hatchlings from the Azores, the relationship between body size and annual growth was modelled.

Three growth functions were tested, an exponential decay model, a log linear model and a log linear model weighted by number of individuals used in each growth rate estimate. We would expect, *a priori,* that this weighted model would be the most appropriate approach when curve fitting because the literature derived growth estimates were sometimes based on the growth rate of individual turtles, but sometimes mean values for up to 150 turtles in defined size classes were reported. Growth curves were constrained to not drop below 0.58 $cm.yr^{-1}$; the most robust direct measurement of adult growth derived from mark-recapture data of 67 nesting adults (Bjorndal and Meylen 1983). Based on an initial hatchling size of 4.5cm (Dodd 1988), functional curves between body size and age could then be derived from the modelled annual growth functions. Mean size of neophyte nesters from the SE USA (98.2 cm CCL; TEWG 2009) was used to derive mean age at maturity estimates, and mean size at recruitment from pelagic to coastal habitats (53 cm CCL; Bjorndal *et al.* 2000) was used to derive estimates of the mean length of the pelagic phase. Because of intensive tagging efforts at nesting rookeries in the SE USA, unmarked females (without tags or obvious tag scars) were inferred to be putative first time nesters since the probability of a female turtle not being detected on a well monitored beach during her first nesting seasons is low.

Reptile age at maturity

All past age at maturity estimates for loggerhead turtle populations along with the most recent age at maturity estimates for other reptile species were drawn from the published literature (Table S3 in Appendix 1). Data from both sexes were included by taking arithmetic means of age and straight carapace lengths (Testudines), published mass estimates (Dinosaurs) and snout vent lengths (Squamates and Crocodilia). Lengths were then converted into mass based on species specific length mass relationships when available, else higher family/order level equations were used. Linear models were fitted to logged mass and age at maturity values for Testudine (turtle/tortoise) and Squamate (snake/lizard) species to investigate age and mass at maturity patterns between and within different reptile orders. All values were used to fit linear models including for the Testudines, the three negative outliers that were more in align with the data from the Squamates.

Results

Drifter derived growth estimates

In the North Atlantic, a total of 96 buoys passed within 50km from the East coast of the USA (Florida to North Carolina). Drift calculations to Northern Europe were based on 15 buoys, which completed leg 1 of this journey (drift time: 337 ± 266 days [mean ± SD]) and 34 buoys that completed leg 2 of this journey (439 ± 176 days). Drift calculations to the Azores were based on 22 buoys that completed leg 1 of this journey (301 ± 280 days) and 54 buoys that completed leg 2 of this journey (436 ± 387 days; Fig. 1a). In the North Pacific, a total of 385 buoys passed within 50km of nesting beaches in Japan. Drift calculations to the area of high seas where turtle size data were derived were based on 83 buoys which reached this area (leg 1; 320 ± 190 days) and the time these 83 buoys spent in this area before continuing along their trajectories in the North Pacific gyre (leg 2; 323 ± 265 days; Fig. 1b).

By combining all possible combinations of leg one and leg two drift times over 500 (15 leg one buoys × 34 leg two buoys), 1000 (22 × 54) and 6000 (83 × 83) possible drift time scenarios were calculated from Florida to the UK/France, Florida to the Azores and Japan to the central North Pacific respectively. These calculations produced modal drift times for these three journeys of 650, 450 and 550 days respectively (Fig. 1c). Based on the modal drift time to the Azores, adding 1, 2 and 3 $hr.d^{-1}$ of directional swimming

oriented by the geomagnetic field to the centre of the gyre (as described by Lohmann *et al.* 2001) lead to predicted increases in drift times of 45, 64 and 94 days respectively.

Size of loggerhead turtles

Size data were available for a total of 273 loggerhead turtles encountered around the coast of the UK/France, 2318 individuals from the Azores and 52 from the Pacific. It was not always clear whether measurements were based on straight (SCL) or curved carapace lengths (CCL). However, we included all reported carapace lengths since our interest was on small turtles (c.20 cm) in length and absolute differences between CCL and SCL of specimens is small and likely why distinctions between the two measurements are often not made (Witham and Futch 1977). In northern Europe, stranded loggerhead turtles ranged in size from 4.7 cm to 110.0 cm carapace length with a clear predominance for small turtles (≤25.0 cm, n = 244). For these turtles stranding in Northern Europe, the midpoint (20.0 cm) of the modal size class of small turtles was used to best represent size at arrival following direct drift from the SE USA (Fig. 2a).

The Azores and North Pacific are important pelagic development habitats in which turtles take up temporary residency upon arrival. The modal size class of small turtles encountered is thus not an accurate representation of size at first arrival since turtles spend protracted periods in these areas. For the Azores, the smallest turtles encountered were <15.0 cm (n = 9) and the first size class that turtles started to arrive in appreciable numbers was ≥15.0 to <20.0 cm (n = 150). Consequently, while the abundance of turtles peaked in the size class ≥20.0 to <25.0 cm (n = 405), we considered the size of first drifters to arrive from SE USA to be best represented by the mid-point (17.5 cm carapace length) of the smallest size class at which comparatively appreciable numbers of individuals were recorded (Fig. 2b). The size of turtles in the North Pacific ranged from 13.0 cm to 63.0 cm in carapace length. Within this size range, two size stages of turtles were apparent, those <30.0 cm carapace length (n = 8) and those ≥30.0 cm carapace length (n = 44). Mean size of the group of 8 small turtles (19.0 cm) was used to best represent the size of the first turtles to drift from Japan to this high seas site (Fig. 2c). Based on mean size at hatching (Dodd 1988) and combining the increase in size of the individuals (between hatching and re-encounter) with the calculated modal time to travel between the respective sites, we estimate growth rates of post-hatchling loggerhead turtles travelling to northern Europe, the Azores and the central North

Pacific of 8.7 cm.yr^{-1}, 10.5 cm.yr^{-1} and 9.6 cm.yr^{-1} respectively (however, see Table S2 in Appendix 1 for the range of growth estimates based on different sizes at arrival and drift times).

Growth/age at size curves

We found 27 published studies presenting growth rate estimates for loggerhead turtles; 21 of which were conducted in the North Atlantic/Mediterranean, one in the North Pacific and five in the South Pacific (Table S3 in Appendix 1). For the North Atlantic, six studies contained growth rate estimates with suitable mark-recapture intervals that enabled size-specific annual growth to be determined. Furthermore, Lagrangian estimates of drift times from Florida to the Azores (450 days) from which we derived growth rates ensured that problems with long growth intervals for parameterising nonlinear growth functions were avoided.

Data from six marked individuals ranging in size at first capture from 26.0 cm (CCL) to 78.4 cm (CCL) came from turtles utilising development habitats around the Azores. Data from seven marked individuals ranging in size at first capture from 55.0 to 83.4 cm (CCL) were recaptured in neritic habitats off the coast of North Carolina. Mean size and growth rate data based on 104 individuals spanning three size classes (from 50.0 to 79.0 cm CCL) off the coast of North Carolina were also available as was mean size and growth rate data from 67 mature turtles nesting in Florida. A chance stranding event of six alive or freshly dead post-hatchlings following a storm in the Azores prompted the only other estimate of post-hatchling growth since Hays and Marsh's (1997) Lagrangian derived estimate for cold stunned turtles stranding in Northern Europe. By adopting a similar approach to us, Bjorndal *et al.* (2000) used mean hatching date in the SE USA along with mean date of stranding to infer a drift time and hence growth rate estimate of 12 cm.yr^{-1} for turtles with a CCL of 7.3 cm.

The non linear relationship between growth rate and body size was modelled using data that encompass the full spectrum of loggerhead turtle size classes from hatchling (4.5 cm CCL) to mature adults (>98.2 cm CCL). Growth rates decreased markedly with increasing body size, and all three models produced a good fit to our data. The exponential decay model: growth rate (cm.yr^{-1} CCL) = 15.0 × exp (-CCL/36.0) -0.38 ($R^2 = 0.94$, $F_{3,17} = 181$, $P < 0.001$; Fig S1a in Appendix 1) and log linear model: growth

rate ($cm.yr^{-1}$ CCL) = (-10.4 × $\log_{10}$ CCL) + 21.1 (R^2 = 0.95, $F_{1,18}$ = 310, P <0.001; Fig S1b in Appendix 1) explained 94-95% of growth rate variance. However, the relationship was best described by a weighted log linear model which explained 98% of growth rate variance: growth rate ($cm.yr^{-1}$ CCL) = (-10.6 × $\log_{10}$ CCL) + 21.5 (R^2 = 0.99, $F_{1,18}$ = 1701, P <0.001; Fig. 3a).

Using these size-specific annual growth functions, we derived size at age curves. A broad range over the size at maturity was evident amongst neophyte nesters along the SE coast of USA (98.2 ± 5.5 [mean ± SD], range: 80.4-115.0 cm CCL, *n*=826; TEWG 2009); consequently, mean size at first maturity was used to derive mean age at maturity. Using this size, mean age at maturity is estimated at 42.4 years (exponential decay model: 95% CI 30.1-60.0; Fig. S3c in Appendix 1), 44.1 years (log linear model: 95% CI 36.2-52.5; Fig. S3d in Appendix 1) and 45.0 years using our most robust (weighted log linear model: 95% CI 38.0-52.0; Fig. 3b). These three similar estimates are all higher than previous estimates (see Fig. S3 and Table S4 in Appendix 1). Differences in age at maturity estimates derived from parameterisation of log linear weighed models with different growth rate estimates (incorporating directional swimming, different sizes at arrival and drift times) ranged from 43.0 to 47.0 years (Table S2 in Appendix 1).

Using a mean size at recruitment to coastal habitats of 53cm CCL (Bjorndal, *et al.* 2000), mean age at recruitment is estimated to be 7.6 years (exponential decay model: 95% CI 6.6-9.0; Fig S3c in Appendix 1), 7.7 years (log linear model: 95% CI 6.0-8.8; Fig S3d in Appendix 1) and 8.0 years (weighted log linear model: 95% CL 8.0-9.0; Fig 3b) supporting the previous estimate of 8.2 years (Bjorndal *et al.* 2000). Confidence intervals around modelled size at age curves were smallest for juvenile and sub-adult size classes for all three models and increased as individuals reached mean size at maturity. For example, the ranges of age between upper and lower confidence limits were <1 year for all three models for turtles between 4.5 and 40 cm, and for our most robust weighted log linear model (which had the lowest 95% CI range) this increased to < 5 and 14 years for 80 and 100cm CCL turtles respectively (Fig. S2 in Appendix 1).

Reptile age at maturity

Age and mass at maturity data were obtained for a total of 43 Squamate species, 31 Testudine species and for five other large bodied reptile species (two from the Crocodilia order and three from the superorder Dinosaurian) (Table S4 in Appendix 1). Squamate species ranged in mean body mass at maturity from the desert night lizard (*Xantusia vigilis*) at <0.1 g to the Komodo dragon (*Varanus komodoensis*) at 65.0 kg. Testudine species ranged in mean body mass at maturity from the loggerhead musk turtle *(Sternotherus minor)* at 0.1 kg to our loggerhead sea turtle estimate of 95.5 kg. The mass of other large extinct and extant reptile species ranged from the Mississippi alligator (*Alligator mississippiensis*) at 24.2 kg to the *Tyrannosaurus rex* at 2500.0 kg.

Across different reptile taxa, mean age at maturity tended to increase with mean mass at maturity. However, the form of this relationship differed between these two major reptile orders, revealing that turtle/tortoise species take longer to attain maturity than other reptiles of equal mass (Fig. 4). While higher than previous estimates, our revised age at maturity estimate for loggerhead turtles fits within the general size and age at maturity pattern observed within the Testudine order. This is further evidenced by excluding our loggerhead turtle estimate in the regression between size and age at maturity for Testudine species as our age of maturity estimate of 45 years fits within the predicted age range based on 95% confidence intervals around the regression for other Testudine species (mean: 28.0 years, 95% CI 15.0-50.0; $\log_{10}$ age (years) =1.00 + (0.22 × $\log_{10}$ mass (kg)), $F_{1,28}$ =23.0, R^2 =0.45, P <0.001).

Discussion

It is well known that slow growth and late age at maturity are general attributes of reptiles and a consequence of their ectothermic nature (e.g. Nelson *et al.* 2002). Set against this backdrop, our results suggest that loggerhead sea turtles and Testudine species in general are older at maturity than Squamate species of equal mass. Our revised loggerhead turtle age at maturity estimate stems from the parameterisation of our growth curve with new estimates of post-hatchling growth rates, published sub-adult and adult mark-recapture growth estimates (all with controlled mark-recapture intervals) and improved estimates of size at maturity. Consequently, we consider our best estimate of the mean age at maturity (45 years) to have been derived from the most robust loggerhead growth curve to date and thus valuable for inclusion in across taxa

meta-analysis of age at maturity estimates. Post-hatchling growth rates were inferred from Lagrangian estimates of drift times and size at arrival of small turtles at distant sites following direct drift from nesting sites. In so doing we make two key assumptions, firstly that Lagrangian drifters can be considered to drift in the same way as post-hatchlings sea turtles and secondly that we are able to accurately define size at arrival.

For post-hatchlings stranding in Northern Europe, data on both the size and date of stranded individuals were available. Observed monthly frequencies of stranding events peaked in February, March and April, and expected monthly frequencies of stranding events (based on randomly generated normal distributions of Lagrangian drift times to the UK and mean day of hatchling) peaked in March, April and May. These broadly similar seasonalities support assumptions that post-hatchling drift times reflect passive Lagrangian drift. However, the slightly earlier seasonal peak in observed turtle stranding may reflect the fact that some post-hatchlings wash up earlier than expected based on passive drift alone following winter storms. Nevertheless, while hatchlings are known to drift passively with ocean currents (Witherington 2002), recent laboratory experiments have revealed that post-hatchlings are smart drifters that can orientate in response to the intensity and inclination of the geomagnetic field (Lohmann *et al.* 2001; Lohmann *et al.* 2008; Putman *et al.* 2011).

The ability to orientate to the geomagnetic field is presumed to help drifting hatchlings remain in favourable development habitats within the North Atlantic Gyre because observed directional swimming is significantly orientated towards the centre of the ocean gyre. To date, the smallest turtles that have been successfully tracked are much larger (c. 300g) than neonate turtles (c. 20g). Because the details of this "neonate satellite tracking project" are currently unpublished (see however perspectives article by Pennisi 2011) it has not yet been determined whether the movements of these juveniles deviate from surface currents. Nonetheless, by placing realistic hatchling swimming behaviours observed from laboratory experiments into passive particle trajectories, we investigated the impacts that directional swimming may have on drift times and ultimately age at maturity estimates. When incorporating realistic directional swimming into growth rate estimates, our estimated age at maturity increased by just 1.0 years. Since active swimming in response to the geomagnetic field is not orientated towards or

away from our end points, impacts of directional swimming on growth and age at maturity estimates appear to be limited although our age at maturity estimates are considered conservative.

Along with estimating the age of post-hatchlings upon arrival at distant sites, which we accomplished using drift times (see above), the second key input to our post-hatchling growth rate calculation was estimating the size of hatchlings at arrival. Growth rate was then simply the size increase divided by age. For turtles found in northern Europe, there is a very clear modal size (20.0 cm). The most parsimonious explanation for this observation is that these post-hatchlings strand following direct drift from rookeries on the east coast of the USA (Hays and Marsh 1997), with the small numbers of larger juveniles expected to have arrived following more circuitous trips across the Atlantic. Around the Azores and in the North Pacific, turtles of a broad range of sizes are encountered, consistent with the view that upon arrival turtles remain at these sites which are utilised as foraging and developmental habitats. Hence, the smallest size at which comparatively large numbers of individuals were recorded was considered to best represent size at arrival. We are therefore confident that for each location we are using the best available estimates of size at arrival. Furthermore, our Lagrangian derived growth rates support previous estimates of the age of small turtles in both the North Atlantic and North Pacific (Zug *et al.* 1995; Bjorndal, *et al.* 2000) and help complete a general model that explains the vast majority (98 %) of the variation in size-specific growth rates for loggerhead turtles. Nevertheless, for the Azores a range of sizes at arrival and associated growth rate estimates were used to derive size at age curves producing a narrow range of mean age at maturity estimates of 43.0 to 47.0 years.

Whilst much discussion remains over the suitability of different growth equations to derive growth and size at age curves of species (Day and Talor 1997; Karkach 2006; Lee and Werning 2008), by using data from post-hatchlings to mature adults, we avoid the common practice of extrapolating models beyond empirical size ranges. In so doing, all three of our fitted growth curves provided similar mean age at maturity estimates adding to the robustness of our results. Furthermore, our size at age curves closely matched that of the von Bertalanffy growth curve conforming to the relationship found for other large bodied turtle/tortoise species (Gaymer 1968; Frazer and Ehrhart 1985; Frazer, *et al.* 1990). The error associated with 95% CI around age at size estimates was

lowest for the weighted log linear model, demonstrating the utility of this modelling approach to derive age at maturity estimates. This error increases with increasing body size; an unavoidable property of a non linear growth model that approaches close to zero prior to maturity as opposed to a sign of weaker parameterisation of the growth rates of large adults.

Age at maturity estimates are typically based on the mean size of breeding populations. However, for species with indeterminate growth patterns, it is necessary to discriminate between first time breeders and the rest of the nesting population to get reliable age and size at maturity estimates (e.g. Hawkes *et al.* 2005). Size at maturity can be highly variable for highly migratory and/or circumglobal species such as sea turtles due to variation in growth rates prior to maturity (Angilletta Jr *et al.* 2004; Angilletta Jr, *et al.* 2004; Schaefer and Walters 2010). Mean size of neophyte nesters from well monitored beaches such as the SE USA thus provided the best indication of size at maturity and was used in our study.

Previous estimates of the mean age at which loggerhead turtles attain sexual maturity show a systematic shift from early estimates based on growth rates in captivity (<10 years) to a progressive upward revision of this estimate (to 39 years). This shift occurred as the slower growth rates of free-living animals became apparent through mark-recapture efforts. Our age at maturity estimates are thus in accordance with this trend and highlights the importance of the continual revision of age at maturity estimates as better data and techniques become available.

Furthermore, our revised estimate of 45 years based on a mean size of maturity of 98.2 cm CCL (TEWG 2009) supports the past highest mean age at maturity estimate of 39 years for North Atlantic populations (NMFS-SEFSC 2001) using a mean size at maturity of 97.2 cm CCL. This former estimate was derived from a growth curve using mark-recapture data of subadult turtles (≥ 50 SCL cm) that had recruited from pelagic to coastal habitats with re-capture intervals of > 0.9 years. Duration of the pre-recruitment pelagic stage was defined as 7 years based on length frequency analysis of pelagic turtles around the Azores and a chance storm driven stranding event of seven post-hatchling turtles (Bjorndal, *et al.* 2000). Our Lagrangian drifter derived post-hatchling growth estimate which stemmed from 1188 drift scenarios and 150 stranded post-

hatchlings supplements the storm derived post-hatchling growth estimate of Bjorndal *et al.* (2000) resulting in the most robust growth curve to date in terms of the parameterisation of juvenile life stages. Furthermore, while sub-adult and adult growth rate estimates are now routinely derived from mark-recapture intervals of $\geq$ 0.9 year because of growth seasonality, we also included an upper limit of 4 years on mark-recapture intervals. Placing an upper limit on mark recapture intervals should also be routine practice for species that exhibit non linear growth trajectories as size specific growth rates are overestimated from long recapture intervals resulting in a tendency to underestimate age at maturity.

Inclusion of our loggerhead age at maturity estimate with that of 78 other reptile species revealed strong positive relationships between mean mass and mean age at maturity within the Squamate and Testudine orders. However, it is striking that the time taken for turtle/tortoise species to reach maturity is much longer than other large bodied snakes, lizards, crocodiles and dinosaurs. Whilst the reasons behind these differences are enigmatic, the finding of later age at maturity raises concerns over the future sustainability of turtle and tortoise populations, because age at maturity is one of the most important predictors of extinction risk for k-selected species where population trends are largely driven by survival rates of mature individuals (Gadgil and Bossert 1970; Heppell, *et al.* 2000; Saether and Bakke 2000; Fujiwara and Caswell 2001; Linares *et al.* 2007; Eldridge *et al.* 2010).

For logistical reasons, monitoring efforts for threatened sea turtle species are directed at breeding grounds; this may, however, be a poor indicator of the status of populations due to the long maturation times highlighted by our study and the resultant time lag before population declines or changes such as climate altered sex ratios would be detectable in the breeding stock (Davenport 1997; Wapstra *et al.* 2009; Witherington *et al.* 2009; Schwanz *et al.* 2010). In light of this ticking time bomb scenario, further precautions need to be built into management regimes. Our findings coupled with more comprehensive datasets and understanding of turtle life histories present a timely opportunity to revise growth curves and age at maturity estimates for other sea turtle populations using novel and more refined methodologies such as those advocated here. Furthermore, by highlighting the ease with which expanding Lagrangian datasets can be used to shed light on the ecology (in this instance growth rates) of species during life-

history stages where more conventional approaches have struggled, it is hoped its use will have broader application amongst the wider marine community.

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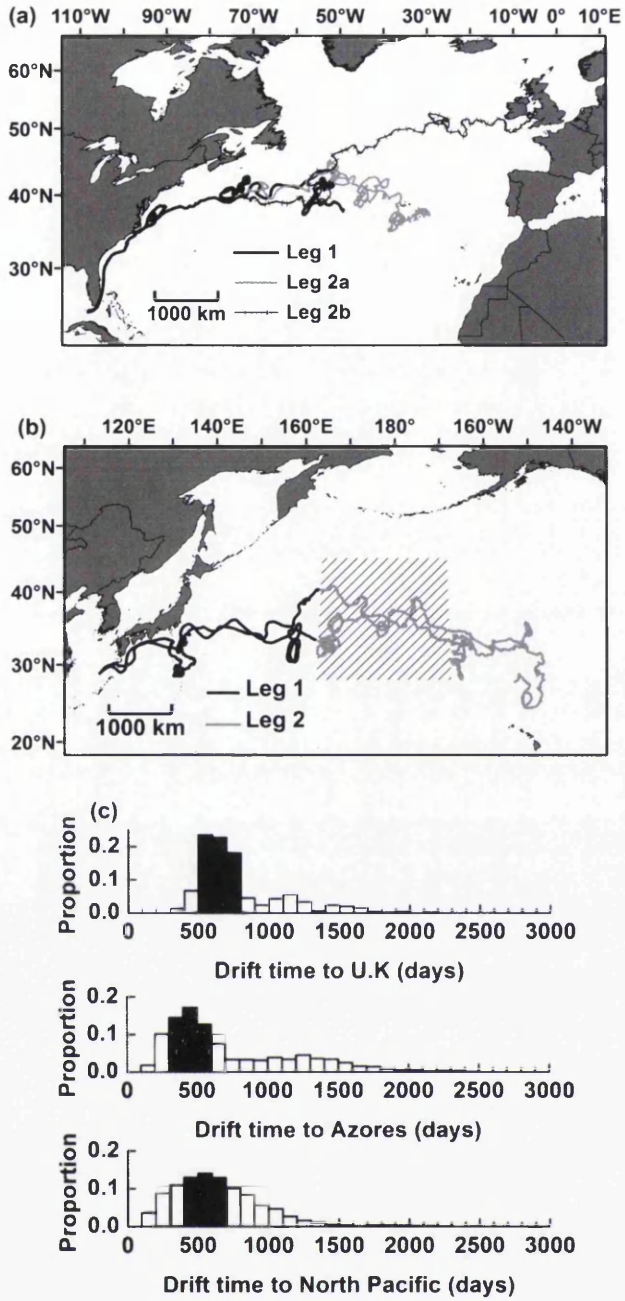

Fig. 1. Lagrangian-derived drift times. (a) Example of buoy trajectories used to estimate drift times to Northern Europe (UK/France) and the Azores. Black line (leg 1) shows example trajectory of a buoy reaching the area of the North Atlantic (45°N, 55°W) where buoy trajectories split either towards the UK (leg 2b) or towards the Azores (leg 2a). (b) Example buoy trajectories used to estimates drift times to the oceanic North Pacific (hashed box). Leg one shows example trajectories of buoys that reach this oceanic area, and leg two shows example trajectories of the same buoys passing through this area. (c) Histograms showing modal drift time classes from which mid-points were used in analyses to best represent the time interval between hatching and re-encounter (black bars). All combinations of leg one and leg two drift times were used to generate histograms.

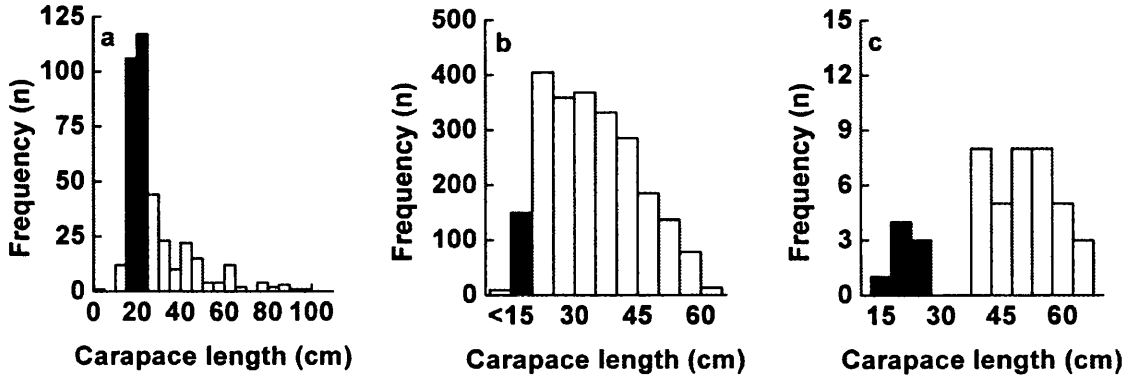

Fig. 2. Length frequency distributions of loggerhead sea turtles encountered around the coasts of Northern Europe (a), the Azores (b) and in the North Pacific (c). Black bars indicate size classes used to best represent first hatchlings to arrive in large numbers from nesting locations in the SE USA (a/b) and Japan (c) for which mid points (a/b) or means (c) were used to derive growth rate estimates.

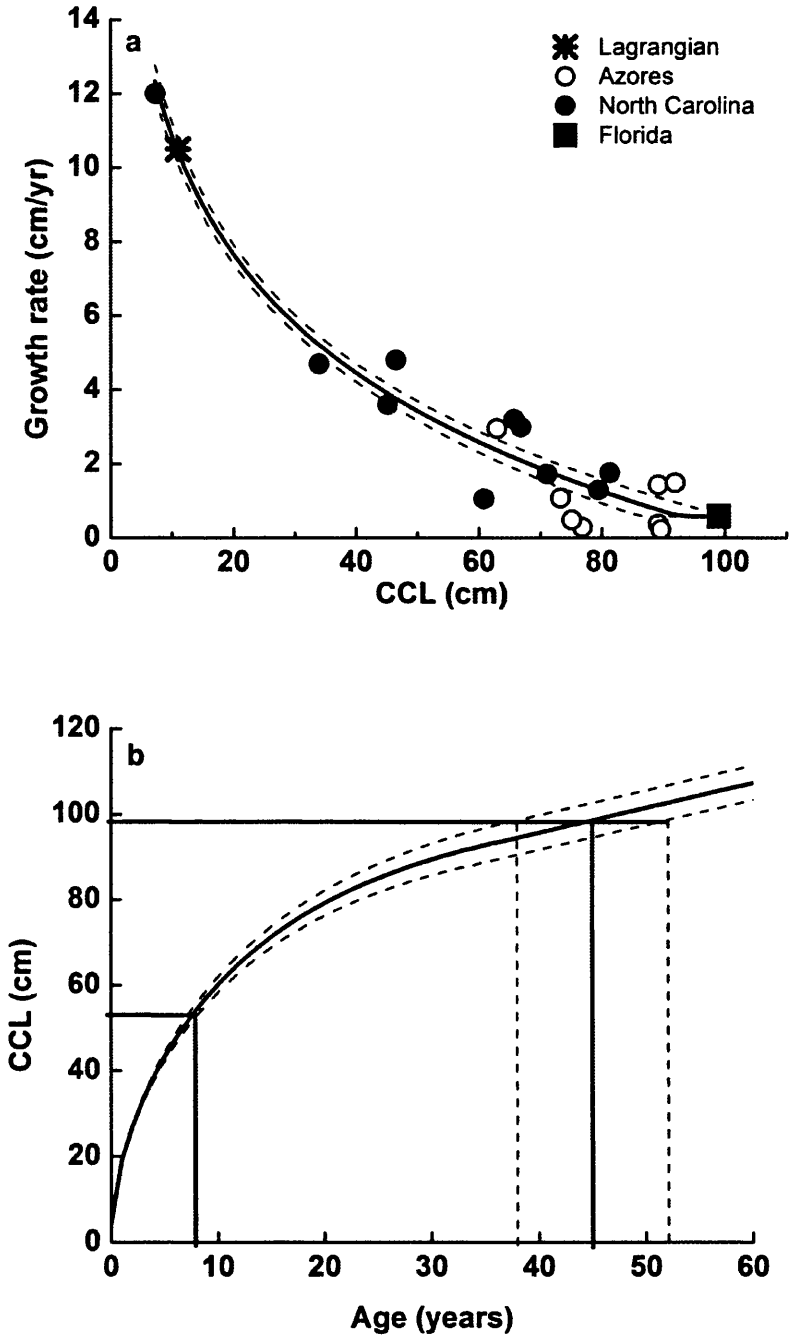

Fig. 3. Western Atlantic loggerhead turtle growth (a) and size at age curve (b). (a) Line fitted from weighted log linear model: growth rate ($cm.yr^{-1}$ CCL) = (-10.6 × $\log_{10}$ CCL) + 21.5 (R^2 = 0.99, $F_{1,18}$= 1701, $P < 0.001$). Lagrangian: growth estimate from our study; Azores: growth estimates for small turtles arriving at the Azores; North Carolina: mark-recapture data of large juveniles; Florida: mark-recapture data of nesting females (b) Mean age at recruitment to coastal habitats is estimated to be 8.0 years (based on a mean size at recruitment of 53 cm CCL; 95% CI 8.0-9.0) and mean age at maturity is estimated to be 45.0 years (based on a mean size at maturity of 98.2; 95% CI 38.0-52.0).

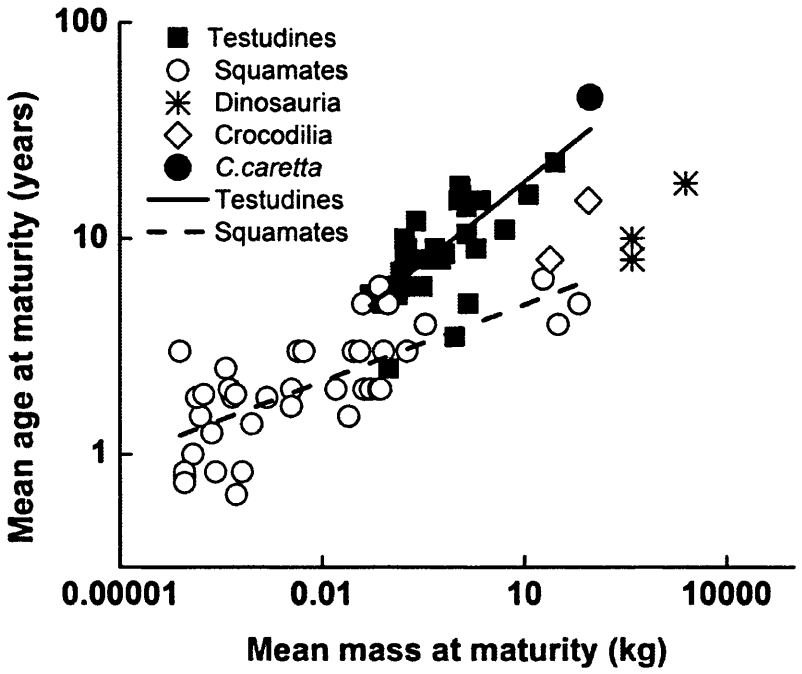

Fig. 4. Meta-analysis of age and size at maturity values plotted on logged axes for a range of extinct and extant reptile species. Linear regression reveals that our estimated age and mass at maturity of loggerhead turtles fits within the life-history patterns observed for other members of the Testudines order. Also highlighted is the fact that turtles/tortoises take longer to reach maturity than lizards/snakes. Testudines: $\log_{10}$ age (years) = (0.25 × $\log_{10}$ mass (kg)) + 1.00 ($F_{1,29}$ = 39.1, R^2 = 0.56, P < 0.001). Squamates: log10 age (years) = (0.12 × $\log_{10}$ mass (kg)) + 0.57 ($F_{1,41}$ = 46.4 R^2 = 0.53, P < 0.001). The regression coefficients between these two regressions were significantly different (T = 2.98, P = 0.004, d.f. = 1).

Appendix 1

Fig. S1. Western Atlantic loggerhead turtle growth (a/b) and size at age curves (c/d). (a) Line fitted from exponential decay model. Growth rate ($cm.yr^{-1}$ CCL) = 15.0 × exp (-CCL/36.0) -0.38 (R^2 = 0.94, $F_{3,17}$ = 181, P < 0.001). (b) Line fitted from log linear model. Growth rate ($cm.yr^{-1}$ CCL) = (-10.4 × $\log_{10}$ CCL) + 21.1 (R^2 = 0.95, $F_{1,18}$ = 310, P < 0.001). (c) Mean age at recruitment to coastal habitats and maturity derived from model (a) is estimated to be 7.6 years (95% CI 6.6-9.0) and 42.4 years (95% CI 30.1-60.0). (d) Mean age at recruitment to coastal habitats and maturity based on model (b) is estimated to be 7.0 years (95% CI 6.0-8.8) and 44.1 years (95% CI 36.2-52.5). See Table S3 for references.

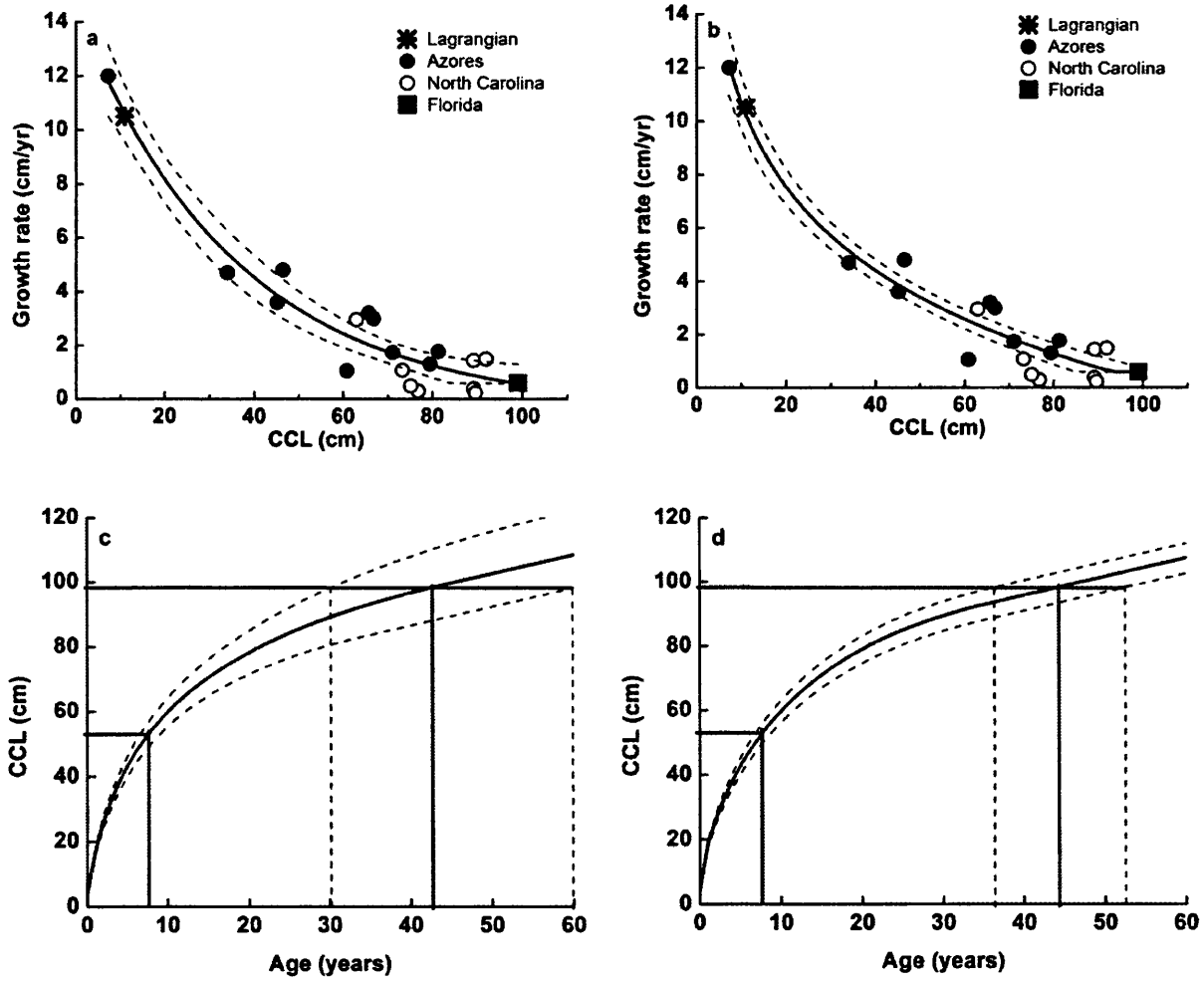

Fig. S2. Difference in age at size estimates based on 95% confidence intervals. Our most robust model (the weighted log linear model) has the lowest 95% CI range and for all three models this range increases with increasing body size.

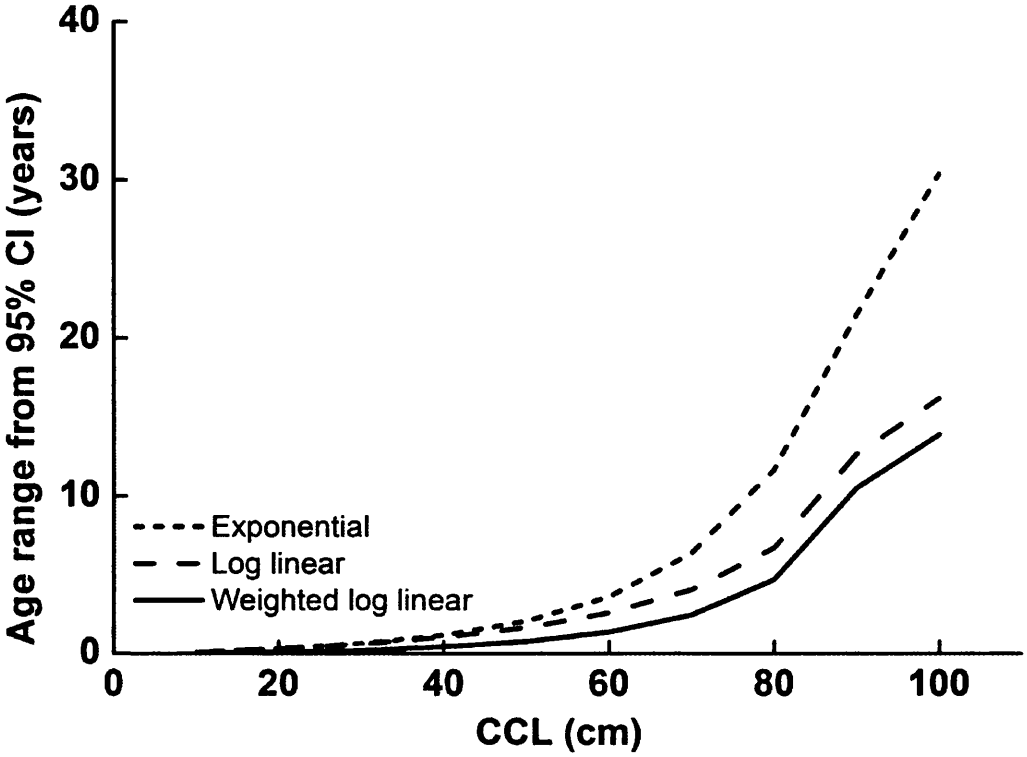

Fig. S3. Meta analysis of published mean age at maturity estimates for loggerhead sea turtles. Our estimate is plotted (black dot) along with all past estimates from Pacific and Atlantic populations and those based on captive growth rates (see Table S4 for references).

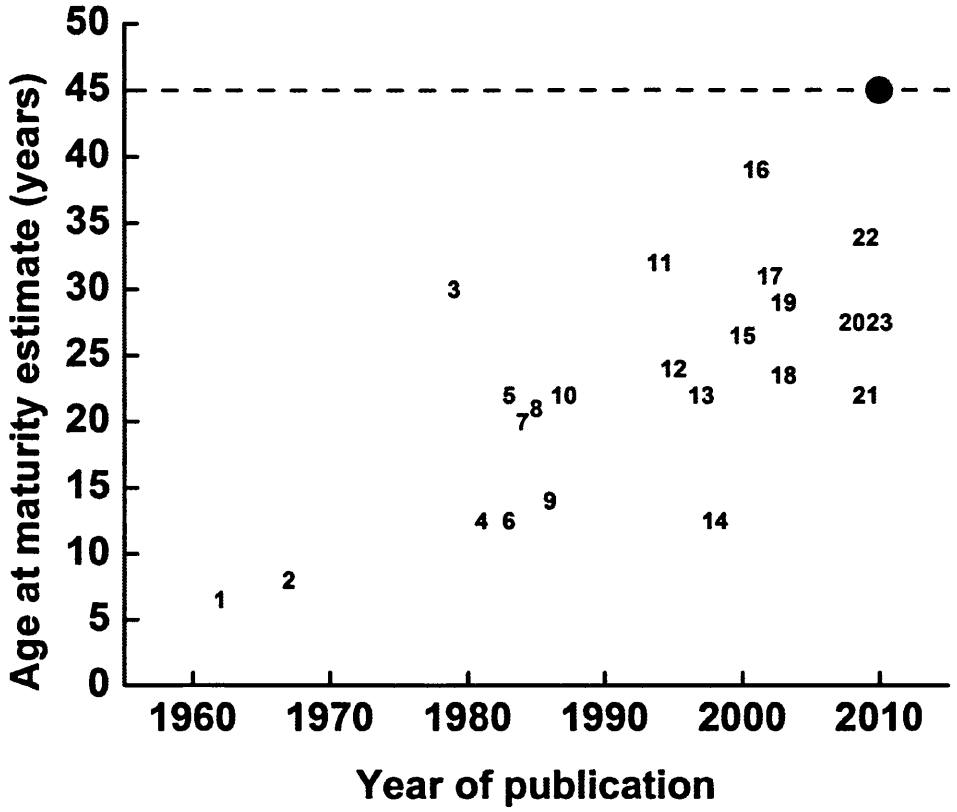

Table S1. Sources from which loggerhead size data were obtained

Encounter location	References
North Atlantic	
United Kingdom:	Marine Environmental Monitoring website: http://www.strandings.com/
France	Brongersma 1972; Duguy 1990; Duguy 1992; Duguy 1993; Duguy 1994; Duguy 1995; Duguy 1996; Duguy *et al.* 1997; Duguy *et al.* 1998; Duguy *et al.* 1999; Duguy *et al.* 2000; Duguy *et al.* 2001; Duguy *et al.* 2002; Duguy *et al.* 2003; Duguy *et al.* 2004; Duguy *et al.* 2005; Duguy *et al.* 2006; Duguy *et al.* 2007; Duguy *et al.* 2008
Azores	Bjorndal *et al.* 2003
North Pacific	Parker *et al.* 2005

Table S2. Error associated with growth rate estimates and age at maturity. Range of growth rate estimates (and associated age at maturity estimates in parenthesis) for the Azores based on different drift times, amounts of directional swimming and size at arrival estimates. Our best estimates of growth rate, size at arrival and drift times used to parameterise our growth curve are denoted with an asterisk.

	Size definition	Min-point of selected size class (fig 2b; black bar)	Mid-point of selected size class (fig 2b; black bar)	Max-point of selected size class (fig 2b; black bar)
Drift definition	**Drift/size values**	15	*17.5	20
Mean of modal drift classes (300 to ≤ 600 days; black bars fig 1b)	447		10.6	
Mean of extended modal drift classes (200 to ≤700 days; fig 1b)	440		10.8 (45.0)	
*Mid-point of modal drift classes (black bars; fig 1b)	*450	8.5 (47.0)	*10.5 (45.0)	12.6 (43.0)
Mid-point of modal drift + 1h.d^{-1} directional swimming	495		9.6	
Mid-point of modal drift + 2h.d^{-1} directional swimming	513		9.2	
Mid-point of modal drift + 3h.d^{-1} directional swimming	544		8.7 (46.0)	

Table S3. Sources of published loggerhead turtle growth rates. A total of six electronic databases were searched (Google Scholar, Scopus, ISI Web of Science, Science Direct, Seaturtle.org and the Marine Turtle Newsletter). All searches used the following search terms: sea turtle, loggerhead turtle, *Caretta caretta*, growth curve, growth rates, mark re-capture. No restrictions on year span were imposed to ensure maximum coverage. References denoted with asterisk's contained suitable data used to parameterise our growth curve for North Atlantic populations.

Study population	**References** (*: used to derive growth curve)
North Atlantic/ Mediterranean	Mendonça 1981; *Bjorndal and Meylen 1983; Zug *et al.* 1986; Bjorndal and Bolten 1988; *Eckert and Martins 1989; Morreale and Standora 1989; Morreale and Standora 1990; Morreale and Standora 1991; Bolten *et al.* 1992; *Klinger and Musick 1992; *Bjorndal *et al.* 1994; Klinger and Musick 1995; Hays and Marsh 1997; Parham and Zug 1997; *Bjorndal *et al.* 2000; Eggers *et al.* 2001; Bjorndal *et al.* 2003; Broderick *et al.* 2003; Snover *et al.* 2007; *Braun-McNeill *et al.* 2008; Casale *et al.* 2009; Casale *et al.* 2009
North Pacific	Hatase *et al.* 2004
South Pacific	Limpus 1979; Limpus 1985; Limpus and Reimer 1992; Limpus 1994; Limpus 1994

Table S4. Sources of reptile age at maturity data. A total of six electronic databases were searched (Google Scholar, Scopus, ISI Web of Science, Science Direct, Seaturtle.org and the Marine Turtle Newsletter). All searches used the following search terms: sea turtle, loggerhead turtle, *Caretta caretta*, age at maturity. No restrictions on year span were imposed to ensure maximum coverage.

	Year (fig, 5 ref no.)	**Reference**
Loggerhead Turtle	1962 (1)	Caldwell 1962
	1967 (2)	Uchida 1967
	1979 (3)	Limpus 1979
	1981 (4)	Mendonça 1981
	1983 (5)	Frazer 1983
	1983 (6)	Zug *et al.* 1983
	1984 (7)	Frazer and Schwartz 1984
	1985 (8)	Frazer and Ehrhart 1985
	1986 (9)	Zug *et al.* 1986
	1987 (10)	Crouse *et al.* 1987
	1994 (11)	Crowder *et al.* 1994
	1995 (12)	Klinger and Musick 1995
	1997 (13)	Parham and Zug 1997
	1998 (14)	Chaloupka 1998
	2000 (15)	Bjorndal *et al.* 2000
	2001 (16)	NMFS-SEFSC 2001
	2002 (17)	Snover 2002
	2003 (18)	Chaloupka 2003
	2003 (19)	Heppell *et al.* 2003
	2008 (20)	Braun-McNeill *et al.* 2008
	2009 (21)	Vaughan 2009
	2009 (22)	Casale *et al.* 2009
	2010 (23)	Wabnitz 2010
Testudines		Gaymer 1968; Shine and Iverson 1995; Ernst and Lovich 2009
Squamates		Wiewandt 1977; Auffenberg 1981; Zug and Rand 1987; Shine and Charnov 1992; Rivas 2000
Dinosauria/Crocodilia		Porter 1972; Lee and Werning 2008

Supporting methods

Ocean Model

The ocean model is based on the Nucleus for European Modelling of the Ocean (NEMO). NEMO is a European modelling community effort to advance ocean modelling for the ocean climate research and operational oceanography through a state-of-art common flexible modelling framework. The National Oceanography Centre, Southampton developed the version of NEMO featured in this study. We used fields from a global 1/4° implementation that resolves oceanic eddies of radii exceeding around 100 km and mesoscale variability of energetic currents, such as the Gulf Stream. In a hindcast spanning 1958-2007 (run ORCA025-N206), the model is forced with atmospheric conditions that combine 6-hourly air temperature, humidity and wind fields from the ERA40 reanalysis (Uppala *et al.* 2005) with climatological radiation and freshwater fluxes from the CORE dataset (Large and Yeager 2009). An initial hindcast of 1958-2001 using this configuration of NEMO, compared favourably with observations of recent Atlantic variability (Grist *et al.* 2010).

Particle Tracking

An efficient analytical method for computing large ensembles of offline trajectories was developed in the 1990s (Blanke *et al.* 2001) and customized as the ARIANE software (http://stockage.univ-brest.fr/~grima/Ariane/) for use with NEMO datasets. The trajectories may be based on time-varying currents and are characterized by depth (whether or not the particles are buoyant), age (since release), and property (e.g. temperature and salinity). The ARIANE method is further described in a similar study investigating migrations of the European Eel across the North Atlantic (Bonhommeau *et al.* 2009). We specified 325 particle release sites in the gulf stream located in a grid 10 to 100 km offshore along the SE coast of Florida between latitudes of 25 to 27° N. Grid spacing was 10 km. Trajectory simulations started in September to coincide with peak emergence of hatchlings from SE Florida (Ehrhart and Witherington 1987). Release sites were selected to cover the range of offshore positions that hatchlings can be expected to reach following the initial swimming frenzy (Wyneken *et al.* 2008). Particles were constrained to remain at the uppermost depth level of 0.5m as hatchlings cannot dive deeply due to their positive buoyancy (Milsom 1975). Advected by a surface velocity field that is updated every 30 days (as a monthly-mean field), particles are tracked for two years and positions of particles and associated water temperature are

recorded every 5 days. Trajectory ensembles were obtained using the same 325 release sites each year between 2000 and 2005, producing a 6 x 2-year "super-ensemble" of Lagrangian trajectories. Particles following trajectories with no added behaviour are hereafter referred to as "inert particles".

Inserting swimming behaviour into particles

All behaviour computations and model output analysis were conducted using R software (R Development Core Team 2009). Swimming behaviour was parameterised based on empirical results reported for newborn loggerhead hatchlings from SE Florida. To model the impact of post-hatchling swimming behaviour on drift times we assumed a swimming speed of 1.13 km h^{-1} based on the mean swimming speed reported for loggerhead turtle hatchlings (Salmon and Wyneken 1987; Witherington 1991). This speed was used to assess the impact of 1, 2, and 3 hours of daily directional swimming (h d^{-1}). Swimming activity of hatchlings has only been monitored during their first week of swimming, during this frenzy and post-frenzy period the amount of daily swimming does not drop below 7 h d^{-1} (Wyneken *et al.* 2008). Whilst the values for daily swimming that we assumed (1-3 h d^{-1}) may be conservative estimates, active swimming is expected to decrease after the post-frenzy period once hatchlings escape predator rich coastal waters and enter the North Atlantic Gyre. The swimming speed of turtles will increase as they grow. The swimming speed value we assumed which is based on neonate hatchlings may thus be a conservative estimate for loggerhead turtles during their first few months at sea.

Swimming direction was parameterized based on the mean orientation responses of 29 hatchlings from SE Florida exposed to the magnetic inclination and intensity fields found off the coast of NE Florida (Lohmann *et al.* 2001). The next point in the North Atlantic gyre for which empirical data of this nature exists is located off SW Europe. Since it is unknown how orientation responses change during the ontogeny of post-hatchlings or between these two regions, we parameterised swimming direction based on the location reached by the majority of inert particles after 6 months of drifting. This location corresponded to a region off the coast of North Carolina where particle trajectories begin to divide and either remain in the gyre or drift towards Northern Europe. Based on the results of Lohmann *et al.* (2001) we assumed that the mean heading of post-hatchlings at this location would be roughly directed towards the centre

of the North Atlantic gyre to prevent advection to Northern Europe. Consequently we added 45 degrees to each of the 29 hatchling headings reported by Lohmann *et al.* (2001) to produce a mean heading of 163° (i.e. directed toward the centre of the gyre) and circular standard deviation of 76°. This distribution was then used to model the orientation behaviour of post-hatchlings. This is a first step in accurately defining the swimming behaviour of hatchlings and more empirical values for swim direction and speed will lead to better parameterisation. Our key objective was simply to take reasonable estimates for limited directional swimming by post-hatchlings to see if this impacts their drift times.

Behaviour simulations were run from the same release sites as the 6-year NEMO ensemble. To insert swimming behaviour into particles at day 5 and for each subsequent 5-day interval during one year, we randomly selected a swimming direction from the distribution detailed above and assumed a swimming speed of 1.13 $km.h^{-1}$. In this way the particles with behaviour (i.e. simulated hatchlings) were "nudged" to a new location. For the current vector for the next 5-days we selected the vector of the closest inert particle within the NEMO ensemble. The resulting position was then again nudged with a new swimming direction from the distribution detailed above and again given a swimming speed of 1.13 $km.h^{-1}$. In this way the "particles with behaviour" trajectories were derived. To determine the influence of 1, 2 and 3 $h.d^{-1}$ directional swimming, behaviour simulations were compared with the passive drift simulations generated in the full 6-year NEMO ensemble. Based on the mean time difference taken to travel west to east in the North Atlantic gyre arising from 1, 2, 3 $h.d^{-1}$ directional swimming Lagrangian drift times to the Azores are adjusted accordingly.

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Chapter 2

A little movement orientated to the geomagnetic field makes a big difference in strong flows

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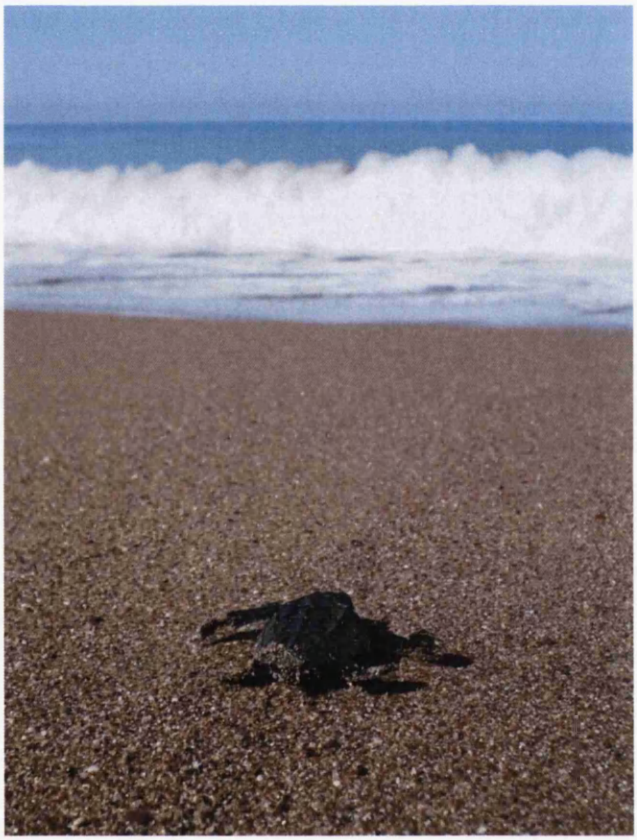

Disclaimer: RS conducted all the analysis in this study. RM set up the ocean model so that RS could compute Lagrangian ocean model trajectories. RS programmed swimming behavior of hatchling turtles into Lagrangian trajectories. RS prepared all the figures and wrote the manuscript with GCH and RM.

Abstract

Whilst a range of animals have been shown to respond behaviourally to components of the Earth's magnetic field, evidence of the value of this sensory perception for small animals advected by strong flows (wind/ocean currents) is equivocal. We added geomagnetic directional swimming behaviour for North Atlantic loggerhead turtle hatchlings (*Caretta caretta*) into a high resolution (1/4°) global general circulation ocean model to simulate 2925 1-year long hatchling trajectories comprising 355,875 locations. A little directional swimming (1-3 hours per day) had a major impact on trajectories; simulated hatchlings travelled further south into warmer water. As a result, thermal elevation of hatchling metabolic rates was estimated to be between 63.3-114.5% after 220 days. We show that even small animals in strong flows can benefit from geomagnetic orientation and thus the potential implications of directional swimming for other taxa may be broad.

Introduction

The use of geomagnetic information has been widely implicated in animal navigation and is supported by evidence from several species showing an ability to respond behaviourally to changes in the Earth's magnetic field (e.g. see review by Wiltschko and Wiltschko 2005). Geomagnetic information can potentially be used to derive positional and navigational cues since magnetic inclination angle and field intensity are particularly pervasive features of the Earth's magnetic field which vary predictably over the majority of the Earth's surface (e.g. see Lohmann *et al.* 2008). For example, orientation responses to manipulated changes in magnetic inclination angle and field intensity have been shown for hatchling sea turtles (Lohmann *et al.* 2001; Merril and Salmon 2010; Putnam *et al.* 2011), satellite tracked adult sea turtles (Luschi *et al.* 2007), lobsters (Boles and Lohmann 2003) and birds (e.g. see review by Wiltschko and Wiltschko 1996). Whilst establishing the value of geomagnetic orientation for larger organisms under natural conditions is possible through direct tracking (Luschi *et al.* 2007), this is challenging for smaller species, or smaller development stages of large taxa, since high-resolution direct tracking of small individuals for extended periods is generally not feasible due to size constraints of transmitters.

Even very small organisms only mm or cm in size may move very large distances (10, 100 or 1000 s of km). For example, many small organisms may be carried long distances by a moving environment, i.e. air flows for aerial animals (and plants) and currents for aquatic species. Whilst such small organisms are notoriously difficult to track directly, it is known that they can employ mechanisms to help favourable dispersal. For example, plants may release seeds and insects may chose to fly when winds are favourable (Nathan *et al.* 1999; Jongejans *et al.* 2007; Brattström *et al.* 2008). In addition, it has been suggested that organisms may modify their behaviour while being carried along by their environment (i.e. air/water) and thereby impact their migrations and destination. The two main mechanisms for altering trajectories are to correct for drift displacements by changing heading (Chapman *et al.* 2010) or by vertical movement into different (more favourable) horizontal water or air flows (Kristiansen *et al.* 2009). Over large spatial scales (both in air and in water), directional movement in response to the ambient geomagnetic field may, in theory, help animals to arrive at more favourable destinations. This scenario has been implicated for one group of widespread and paradigmatic long-distance ocean travellers, the sea turtles.

For North Atlantic loggerhead turtle hatchlings (*Caretta caretta),* elegant laboratory experiments have revealed directional swimming in response to two components of the geomagnetic field, inclination and intensity (Lohmann *et al.* 2001; Merrill and Salmon 2010; Putman *et al.* 2011). Together, these components have been proposed to provide a bi-coordinate map operating across ocean basins. These laboratory experiments have shown that, broadly speaking, hatchlings adopt a swimming direction that would aid with entrainment in the North Atlantic gyre, and this use of geomagnetic navigational signposts has been proposed to help post-hatchlings stay within favourable conditions. Direct testing of this idea is, however, difficult since it is impossible to directly track hatchlings for extended periods and to have a group of control animals and experimentally disturbed animals (e.g. using the classic set-up of placing magnets on the body to disrupt perception of the geomagnetic field). Hence, alternative approaches are needed to test the impact of directional swimming by hatchling turtles.

We calculate a 6 × 2-year "super-ensemble" of passively drifting (from hereafter referred to as inert particle) trajectories from the surface current fields of a state-of-the-art ocean model hindcast. By placing realistic swimming behaviours into inert particles, we investigate whether directional swimming may be used profitably by sea turtles, not simply when they are large powerful swimmers, but also during their first year of life, when they enter the sea as small hatchlings.

Methods

Ocean Model

The ocean model is based on NEMO, the Nucleus for European Modelling of the Ocean. NEMO is a European modelling community effort to advance ocean modelling for the ocean climate research and operational oceanography through a common flexible modelling framework. The version of NEMO featured in this study was developed at the National Oceanography Centre, Southampton. We use fields from a global 1/4° implementation that resolves both the mesoscale variability of energetic currents, such as the Gulf Stream, and oceanic eddies of radii exceeding around 100 km. In a hindcast spanning 1958-2007 (run ORCA025-N206), the model is forced with atmospheric conditions that combine 6-hourly air temperature, humidity and wind fields from the ERA40 reanalysis (Uppala *et al.* 2005) with climatological radiation and freshwater

fluxes from the CORE dataset (Large and Yeager 2009). Using this configuration of NEMO, an initial hindcast of 1958-2001 compared favourably with observations of recent Atlantic variability (Grist *et al.* 2010).

Particle Tracking

An efficient analytical method for computing large ensembles of offline trajectories was developed in the 1990s (Blanke *et al.* 2001), and the method has been specifically customized as the ARIANE software (http://stockage.univ-brest.fr/~grima/Ariane/), for use with NEMO datasets. The trajectories may be based on time-varying currents and are characterized by age (since release), depth (whether or not the particles are buoyant) and property (temperature and salinity). The ARIANE method was recently used in a similar study, to investigate migration of the European Eel across the North Atlantic, and is further described in that paper (Bonhommeau *et al.* 2009). We specify 325 particle release sites located in a grid 10 to 100 km offshore along the SE coast of Florida between latitudes of 25 to 27° N. Grid spacing was 10 km and all start points were located within the Gulf Stream. Start date for the trajectory simulations were at the end of September, coinciding with peak hatchling emergence from beaches on SE Florida (Ehrhart and Witherington 1987). Release sites were selected to cover the range of positions that hatchlings are expected to reach offshore following the initial swimming frenzy and post-frenzy period (Wyneken *et al.* 2008). Particles were constrained to remain at the uppermost NEMO depth level of 0.5 m as post-hatchlings cannot dive deeply due to their positive buoyancy (Milsom 1975). Advected by a surface velocity field that is updated every 30 days (as a monthly-mean field), particles are tracked for two years in all cases. Positions of particles and associated water temperature are recorded every 5 days. Trajectory ensembles were obtained using the same 325 release sites each year between 2000 and 2005, producing a 6 x 2-year "super-ensemble" of Lagrangian (drifting particle) trajectories. Particles following trajectories with no added behaviour are hereafter referred to as "inert particles".

Inserting swimming behaviour into particles

All behaviour computations and analysis of model outputs were completed in R (R Development Core Team 2009). Swimming behaviour was parameterised based on empirical results reported for neonate loggerhead hatchlings from SE Florida. From hereafter, we use the term hatchling/neonate to refer to individuals (< 1 week old) and

post-hatchling to refer to individuals (> 1 week old). To model the impact of post-hatchling swimming behaviour on movement trajectories, we first assumed a swimming speed of 1.13 $km.h^{-1}$. This is the mean value reported during active swimming for loggerhead turtle hatchlings (Salmon and Wyneken 1987; Witherington 1991) and was used to assess the impact of 1, 2, and 3 hours of daily directional swimming ($hr.d^{-1}$). Swimming activity of hatchlings has only been monitored during their first week of swimming, during which period the amount of daily swimming does not drop below 7 $hr.d^{-1}$ (Wyneken *et al.* 2008). Hence, the values for daily swimming that we assumed (1-3 $hr.d^{-1}$), may be a conservative estimate. Additionally the swimming speed of turtles will increase as they grow. So again the value we assumed, which is based on neonate hatchlings, may be a conservative estimate for loggerhead turtles during their first year of life.

Swimming direction was parameterized based on the mean orientation responses of 29 hatchlings from SE Florida exposed to the magnetic inclination and intensity fields found off the coast of NE Florida (Lohmann *et al.* 2001). The next point in the North Atlantic gyre for which empirical data of this nature exists is located off SW Europe. Since there is currently no data on how orientation responses change during the ontogeny of post-hatchlings or between these two regions, we chose to parameterise swimming direction based on the location reached by the majority of inert particles after 6 months of drifting. This location corresponded to a region off the coast of North Carolina where particle trajectories start to divide and either remain in the gyre or drift towards Northern Europe. Based on the results of Lohmann *et al.* (2001) we assumed that the mean heading of post-hatchlings at this location would be roughly directed towards the centre of the North Atlantic gyre to prevent advection to Northern Europe. So to achieve this parameterisation, we simply added 45° to each of the 29 hatchling headings reported by Lohmann *et al.* (2001). In this way we produced a mean heading of 163° (i.e. directed toward the centre of the gyre) and circular standard deviation of 76°. This distribution was used to model the orientation behaviour of post-hatchlings. We are fully aware that this is only a first step in accurately defining the swimming behaviour of hatchlings and more empirical values for swim direction and speed will lead to better parameterisation. Our key objective is simply to take reasonable estimates for limited directional swimming by post-hatchlings to see whether this impacts their dispersal.

Behaviour simulations were run from the same 325 release sites as the 6-year NEMO ensemble. To insert swimming behaviour into particles at day 5 and for each subsequent 5-day interval during one year, we randomly selected a swimming direction from the distribution detailed above and assumed a swimming speed of 1.13 $km.h^{-1}$. In this way, the particles with behaviour (i.e. simulated hatchlings) were "nudged" to a new location. For the current vector for the next 5-days, we selected the vector of the closest inert particle within the NEMO ensemble. The resulting position was then again nudged with a new swimming direction from the distribution detailed above and again given a swimming speed of 1.13 $km.h^{-1}$. In this way, the trajectories of "particles with behaviour" were derived. For each 5-day position for the particles with behaviour, ambient sea surface temperature (SST) was determined from the temperature of the closest inert particle in the full 6 × 2-year NEMO ensemble that corresponded to the same month of the particle with behaviour. To determine the influence of 1, 2 and 3 $hr.d^{-1}$ directional swimming, behaviour simulations were compared with the first year of drift from the inert particle simulations generated in the full NEMO ensemble.

Inert particle trajectories were run for 2 years, while "particles with behaviour" were run for only 1 year, since we needed to ensure that the domain of surface current vectors and associated temperatures covered the entire area into which "particles with behaviour" might move. If we had instead run both sets of trajectory for only 1-year, then some of the "particles with behaviour" would move beyond the area covered by the inert particles and hence we would not have baseline current vector data. We chose 1 year for the runs of "particles with behaviour" as this revealed the fate of particle simulations during this critical period, i.e. whether they drifted to Northern Europe or remained in the North Atlantic gyre. Mann-Whitney tests were used to determine if particle latitudes and temperatures arising from different behaviour scenarios were significantly different after c. ¼ year, ½ year and 1 year.

Physiological impacts of thermal environment

The mean latitude and ambient SST experienced every 5 days by each inert particle and each particle with 1, 2 and 3 $hr.d^{-1}$ directional swimming were calculated and ambient SST data smoothed using a monthly moving average function. Using the mean ambient SST every 5 days for each particle, mean relative metabolic rate was estimated based on

the published respirometry-derived relationship between juvenile loggerhead turtle metabolic rate and water temperature (Hochscheid *et al.* 2004): ln VO_2 (in ml O_2. min^{-1}) = -2.87 + (0.168 x SST) – k. Based on the size of the smallest individual from which this relationship was derived, k was set to 0.024. Wilcoxon tests were used to determine if metabolic rates during the first year differed significantly with different behaviour scenarios.

Results

Particle Trajectories

A total of 1950 2-year long Lagrangian trajectories with no behaviour were computed which comprised a total of 284,700 inert particle locations and associated current vectors and water temperatures. The general pattern of trajectories broadly reflected the known currents in the region: particles tended to be carried rapidly NE in the Gulf Stream before streaming eastwards in the North Atlantic Current with some being carried southwards into the Sargasso Sea and others towards Northern Europe. A further 975 1-year long behaviour trajectories were computed (325 with 1, 2, then 3 $hr.d^{-1}$ of directional swimming), comprising another 71,175 particle locations (Fig. 1).

Impacts of Geomagnetic orientation on trajectories

Adding directional swimming to the particles had pronounced impacts on their trajectories (Fig. 2a). The mean latitude of particles initially increased with directional swimming, i.e. during days 10-25 particles with $3hr.d^{-1}$ directional swimming were 1.34 to 0.15° further north than inert particles. This result occurred because during the first 25 days, swimming tended to move particles into the strongest northerly flows of the Gulf Stream quicker than inert particles and hence "particles with behaviour" travelled north faster. After one month (30 days after particle release), "particles with behaviour" have travelled through the strongest northerly flows and a mean SSE swimming orientation starts to lead these particles along more southerly trajectories than inert particles, i.e. by day 30, particles with $3hr.d^{-1}$ directional swimming are 0.13° further south than inert particles. Particles with behaviour travelled progressively further south for the rest of the year with the magnitude of this effect increasing with the amount of daily swimming behaviour.

By December (90 days after particle release), the mean (± SE) latitude of particles with 0h, 1h, 2h and 3hr.d^{-1} of directional swimming behaviour were 37.01°N (± 0.08), 36.44°N (± 0.17), 36.24°N (± 0.18) and 35.85 (± 0.19). So particles with 1-3 hr.d^{-1} of swimming behaviour were on average around 63, 86 and 129 km further south than inert particles. These differences in the mean latitude of particles with behaviour and the inert particles, were all significant ($Z < -4.15$, $P < 0.001$ in all three cases). By March (180 days after particle release), these differences had become magnified: the mean latitude of particles with 0h, 1h, 2h and 3hr.d^{-1} of directional swimming behaviour were 37.58°N (± 0.09), 36.89°N (± 0.21), 36.18°N (± 0.23) and 35.30°N (± 0.24), so on average particles with 1-3 hr.d^{-1} behaviour were around 77, 156 and 254 km further south than inert particles. By day 365, these differences were greater still with the mean latitudes of particles with 1h, 2h and 3hr.d^{-1} of directional swimming behaviour being around 179, 347 and 520 km further south than inert particles. In all cases, these differences in mean latitude after 180 and 365 days between particles with behaviour versus inert particles were again highly significant ($Z < -3.04$, $P < 0.005$ in all cases).

As a consequence of these "particles with behaviour" travelling through more southerly latitudes, their ambient SST was higher than for inert particles (Fig. 2b). This thermal elevation started to become apparent in January (110 days after particle release) and peaked during May (215 days after particle release) when the mean ambient water temperature was 1.5, 2.2 and 2.7°C higher than the mean SST for inert particles (18.7°C) with 1, 2 and 3 hr.d^{-1} of swimming respectively. Again these differences in the mean SST experienced by particles with behaviour versus inert particles were highly significant ($Z < -2.68$, $P < 0.05$ in all cases). So in short, directional swimming led to particles travelling on more southerly trajectories and experiencing warmer water than inert particles, and the magnitude of this effect increased with the amount of daily swimming.

Physiological impacts of thermal environment

The thermal elevation of particles with directional swimming led to a calculated increase in metabolic rate, since metabolic rate increased as a function of water temperature. Again the increase in metabolic rate started to become pronounced during the first winter after particle release. For example, by the end of January, the mean metabolic rate of particles showing 1, 2 and 3 hr.d^{-1} of directional swimming was 9.5,

26.5 and 39.3%, respectively, above the mean metabolic rate of inert particles with no swimming (Fig. 3a). This difference peaked in May when particles were approximately 220 days old, and there was a 63.3 to 114.5% increase in temperature with 1-3 $hr.d^{-1}$ of swimming. When the integrated metabolic rate was calculated over the full year of simulated trajectories, directional swimming equated to an increase of 9.3, 17.0 and 23.3% in metabolic rate with 1, 2 and 3 $hr.d^{-1}$ of swimming (Fig 3b). Mean and integrated metabolic rates over one year were significantly higher for particles with 1, 2 and 3 $hr.d^{-1}$ of behaviour versus inert particles ($Z \geq 7.2$, $P < 0.001$ in all cases).

Discussion

Whilst it is now well established that loggerhead turtle hatchlings can respond behaviourally to changes in magnetic inclination and intensity (Lohmann *et al.* 2001; Merrill and Salmon 2010; Putman *et al.* 2011), it remains equivocal whether such information could only be used profitably by adult turtles when they are large and powerful swimmers able to swim strongly relative to currents (e.g. Luschi *et al.* 2007, Mencacci *et al.* 2010). Set against this backdrop, our results suggest that even relatively limited amounts of directional movement by small post-hatchling sea turtles can influence their trajectory and help individuals to stay within favourable warm water in the North Atlantic subtropical gyre and avoid being advected into cooler more northerly areas where growth and survival is jeopardised.

In addition to our main finding that directional swimming helps post-hatchlings remain at safe latitudes, there may be further advantages. Metabolic rate has been shown to be positively correlated with the growth and fitness potential of other marine ectotherms such as fish (Metcalfe *et al.* 1995). For loggerhead turtle hatchlings, growth rates in captivity have been shown to increase significantly in higher water temperatures between 14-31°C (Hughes 1974; Owens and Ralph 1978) and likewise food intake rates have been shown to increase for juvenile loggerheads kept at temperatures ranging from 15-25°C (Hochscheid *et al.* 2004). Since these temperature ranges correspond to the range from which our metabolic rates were derived, we infer that warmer temperatures encountered in the North Atlantic may produce faster growth rates if food is not limited. Lavage samples have revealed that the diet of SE Florida post-hatchlings is predominantly comprised of members of the Sargassum community and small pleustonic and neustonic organisms which reside at the air-sea interface and are not

associated with Sargassum (Witherington 2002). Whist post-hatchlings show a strong preference for pleuston and neuston (Witherington 2002), knowledge of the distribution and abundance of these organisms which are heavily influenced by wind dispersal is sparse. Consequently, whilst higher SST could potentially be advantageous to post-hatchlings, due to a lack of data on distribution of their prey, it is currently unclear whether thermal elevation would translate into fitness benefits beyond reduced exposure to northerly latitudes and the risks of cold stunning.

The eddy-permitting version of NEMO, on which these results are based, provides a major advance over earlier studies of particle trajectories at basin scales (Hays and Marsh 1997). Such studies relied on model simulations of coarser resolution, incapable of resolving the mesoscale variability in ocean currents that strongly influences the timescales and spreading of passively-drifting particles. The eddy-permitting NEMO simulation reveals rich mesoscale variability, in contrast to a lower resolution counterpart (Marsh *et al.* 2010). Indeed, the trajectories modelled by NEMO show similar patterns to those evident in the trajectories of satellite-tracked buoys (http://www.aoml.noaa.gov/envids/gld/). We are therefore confident that our improved "eddy-permitting" trajectories are a more suitable starting point for the study of swimming behaviour.

Our parameterization of swimming behaviour was based on the available data for neonate hatchlings weighing around 20 g (4.5 cm carapace length) and as such is anticipated to be conservative since swimming performance will change considerably during a year. For example, 1-1.5 year old loggerhead turtles (mean size: 31.6 cm carapace length) followed for up to 4 hours after release from a captive head-starting programme averaged speeds of 1.88 $km.d^{-1}$ (Nagelkerken *et al.* 2003). Clearly, increased swimming speeds will make the difference in the trajectories of inert particles versus "particles with directional behaviour" even more acute. Whilst hatchlings swim almost continuously during the initial 24 hour swimming frenzy, declining to c.7 $hr.d^{-1}$ by the sixth day (Wyneken *et al.* 2008), there is currently no data on daily swimming activity beyond this period. Nonetheless, whilst the strength of hatchlings will improve as body size increases swimming duration can be expected to decline beyond 7 $hr.d^{-1}$ once hatchlings escape the predator rich coastal zone and reach offshore waters where favourable dispersal/development conditions exist. As such, travel distances based on 1-

3 $hr.d^{-1}$ of directional swimming and mean swimming speed of neonates provide the best conservative estimates until better data becomes available.

Whilst the orientation responses of hatchlings exposed to magnetic intensity and inclination values corresponding to the Western and NE boundary of the North Atlantic gyre have been parameterised, it is unclear how orientation responses change as hatchlings travel between these two points. Adopting a single mean heading during the first year of life likely underestimates the ability of post-hatchlings to control their destiny by responding behaviourally to changes in the Earth's magnetic field. However, this approach forms a basis for future work as better data/knowledge of post hatchling swimming behaviour becomes available. By focussing on the first year of life, we cover the critical period when post-hatchlings risk advection to northern Europe and reduced problems associated with the fact behaviour can only be parameterised from experiments conducted on neonate hatchlings, and it is unknown how hatchlings modify their behaviour throughout their ontogeny. Directional swimming is, however, thought to benefit juvenile turtles during the full transatlantic journey, initially by helping post-hatchlings to remain in the favourable development habitat of the North Atlantic and later to return to coastal habitats off the coast of the USA. It is thus hoped that with emerging datasets (e.g. Fuxager *et al.* 2011) that simulations of this nature can be further refined through better behaviour parameterisation and extended beyond the first year. Nonetheless, despite current limitations, our results clearly demonstrate that a very limited amount of swimming can have a big impact on drift scenarios.

In addition to swimming behaviour, the other factor that clearly dictates an animal's trajectory in the ocean is the strength and direction of the current. Here, it should be borne in mind that our simulations started in the very strong flows of the Gulf Stream. This is one of the strongest of the major ocean currents. Our findings that even in these high flows, post-hatchlings can influence their trajectory potentially have much broader implications as elsewhere in the world's oceans where flows are less, the ability of post-hatchlings to influence their movement is likely to be even greater. The swimming ability of loggerhead hatchlings that we used is comparable to other sea turtle hatchlings species (Chung *et al.* 2009). The combination of conservative estimates of swim speed and high current flows in our study area means that our results are likely to provide a

conservative impression of the ability of hatchling sea turtles around the world to influence their trajectory through geomagnetic orientation.

There are a large number of small animals in the oceans that swim actively, yet cannot be tracked, such as fish larvae, small cephalopods and crustacean plankton. Swim speeds of these larvae can be considerably higher than those of loggerhead hatchlings (e.g. Fisher 2005), suggesting that other larval species will be able to influence their destination through active swimming. Placing realistic behaviours into particle trajectories from high-resolution ocean models provides an opportunity to resolve the potential impacts that active swimming by these groups may have. For another transatlantic migrant, the critically endangered European Eel, *Anguilla anguilla,* deriving realistic dispersion patterns in this way is now considered a management priority (Bonhommeau *et al.* 2010). This technique also may serve to identify the potential spread of invasive marine species as they emanate from points of introduction into new environments (Cowen *et al.* 2006). The coupling of accurate parameterisation of organism swimming behaviour and high-resolution ocean general circulation models is thus anticipated to have significant application in the management of a range of species of conservation concern.

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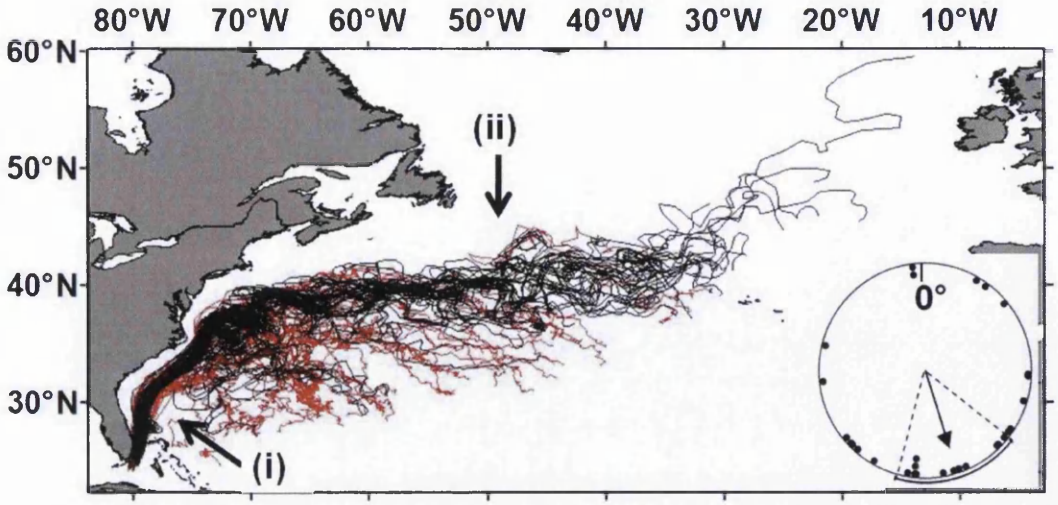

Fig. 1. Paths of a random sample of 50 inert 1-year long particle trajectories (black) and random sample of 50 1-year long particle trajectories with 3hr.d^{-1} directional swimming behaviour (red). The major current systems which border the Sargasso Sea during the first year of drift are indicated (i-Gulf Stream; ii-North Atlantic Current). Inset (bottom right) shows the mean orientation of hatchlings assumed off the coast of North Carolina (this was adapted from empirical results of 29 hatchlings reported by Lohmann *et al.* 2001). This distribution was used to input behaviour into particles by picking a heading at random from this distribution for each 5-day period of active swimming

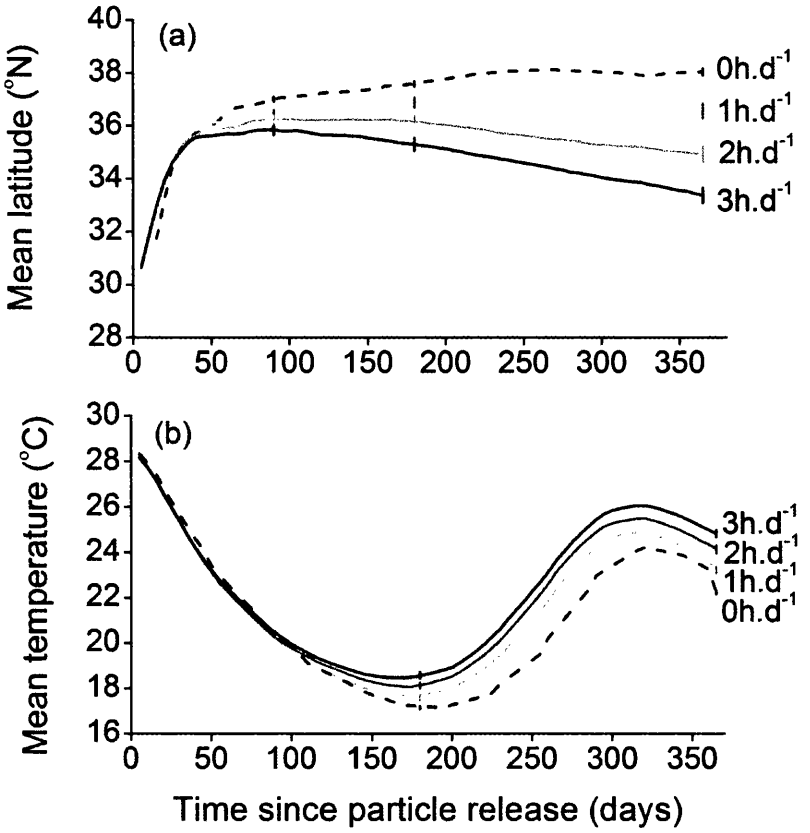

Fig. 2. (a) The mean latitude for particles with no behaviour and 1h, 2h, and 3hr.d^{-1} directional swimming. Mean latitude initially increased with increasing directional swimming, i.e. after 25 days, particles with 3hr.d^{-1} directional swimming were 0.15° further north than inert particles. This occurred because "particles with behaviour" arrived earlier in the strongest northerly flows of the Gulf Stream. After 30 days, particles had travelled through these strongest northerly flows, and directional swimming then led "particles with behaviour" to be progressively further south than inert particles with the magnitude of this effect increasing with the amount of daily swimming behaviour. (b) The mean ambient SST through which particles traversed increased as particles with behaviour travelled more southerly. Ambient SST started to increase after around 100 days which corresponded to the first winter following particle release at the end of September (day 0). Standard error bars are plotted at 180 and 365 days (b) and also for 90 days (a).

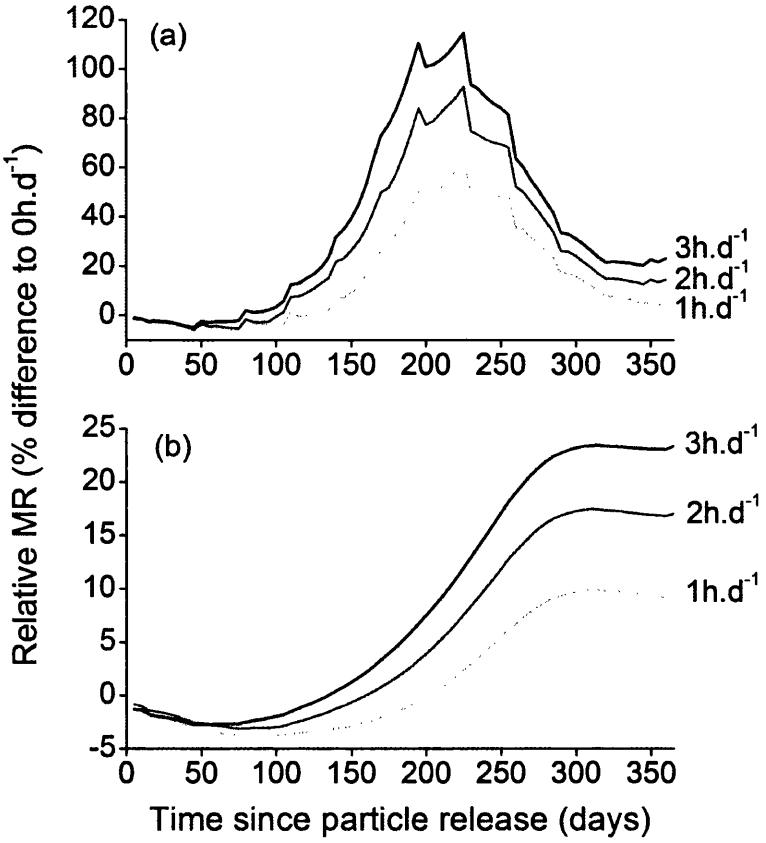

Fig. 3. (a) Relative difference in mean metabolic rate (MR) for particles with 1, 2 and 3 hr.d^{-1} directional swimming compared to particles with no behaviour. MR started to increase during the first winter (c. days 80-110) following release at the end of September (day 0) and was most pronounced (63.3% -114.5% higher with 1-3 hr.d^{-1} respectively) in May when particles were approximately 225 days old. (b) Relative cumulative difference in mean metabolic rate. During February to April (c. days 135-205 with 1-3 h d^{-1} directional swimming respectively), particles start to experience a cumulative increase in MR which then starts to level off in the summer ending with an overall increase of 9.3, 17.0 and 23.3% in MR with 1, 2 and 3 hr.d^{-1} directional swimming, respectively.

Chapter 3

Natal site and offshore swimming influence fitness and long-distance ocean transport in young sea turtles

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Disclaimer: NFP, GCH, and RS conceived the project. PV developed ICHTHYOP software, NFP ran the HYCOM simulations, RM set up the NEMO model so that RS could run NEMO trajectories. NFP and RS analyzed the data, NFP wrote the manuscript with contributions from all authors.

Abstract

Although long-distance transport of marine organisms is constrained by numerous oceanic and biological factors, some species have evolved life-histories reliant on such movements. We examine the factors that promote long-distance transport in a transoceanic migrant, young loggerhead sea turtles (*Caretta caretta*), from the southeastern U.S. Empirical data from near-surface buoys and simulations in two ocean circulation models indicated that passive drifters are often retained for long periods shoreward of oceanic fronts that delineate coastal and offshore waters. Further simulations revealed that offshore swimming aided newly hatched turtles in moving past fronts and increased turtles' probability of survival, reaching distant foraging grounds, and encountering favourable temperatures. Swimming was most beneficial in regions that were more favourable under scenarios assuming passive drift. These results have broad implications for understanding the movement processes of many marine species, highlighting likely retention of more planktonic species and potential for dispersal in more nektonic species.

Introduction

The movement of organisms plays a fundamental role in life-histories, drives the evolution of species by influencing population connectivity, and may influence management of ecosystems such as through the designation of conservation areas (Nathan *et al.* 2008). Recent studies on the movement of individuals in the marine environment have found that local retention typically predominates over long-distance transport, with a number of physical factors serving to keep individuals nearshore (Cowen *et al.* 2006; Cowen and Sponaugle 2009). For instance, increased friction resulting from shallow bathymetry typically reduces current velocities and thus promotes retention (Cowen and Sponaugle 2009). In some locations, such as at the mouths of bays and inlets, tidal flows can result in strong velocities that vertically migrating animals can utilize to achieve horizontal transport shoreward or seaward (Hill 1991). However, even for individuals moving away from the shore, frontal convergence zones that occur at coastal-oceanic boundaries minimize offshore transport (Belkin *et al.* 2009; Cowen and Sponaugle 2009). Submesoscale eddies (10–40 km in diameter) that are often associated with the frontal boundaries of large, fast-flowing currents will further serve to decrease the probability that individuals become, or remain, entrained in large-scale currents that facilitate long-distance movements (Sponaugle *et al.* 2005).

Nonetheless, a number of marine species dispersing from coastal locations have evolved life-histories that rely on long-distance movements, in some cases crossing entire ocean basins (Carr 1987; Azumaya and Ishida 2004; Clarke *et al.* 2003; Luiz *et al.* 2011). Here, we examine the role of swimming behaviour on the movement of a transoceanic migrant-loggerhead sea turtles (*Caretta caretta*). Upon emerging from nests on sandy beaches along the southeastern U.S., hatchling loggerheads enter the sea and swim offshore for a period of hours to days using visual cues, ocean waves, and the Earth's magnetic field to stay on course (Lohmann and Lohmann 2003). This initial ''frenzy period'' is thought to minimize time spent in shallow, nearshore waters where predation risk is likely highest (Wyneken and Salmon 1992; Wyneken *et al.* 2008). After the frenzy period, young loggerheads are typically considered ''passive migrants'' in that they become entrained in the Gulf Stream System and carried to distant foraging areas, such as the Azores (Carr 1987). However, given constraints that impede dispersal in marine organisms, such as shelf-break fronts, mesoscale eddies, and mortality (Largier

2003; Cowen and Sponaugle 2009), it is unclear whether this accepted view of loggerhead life-history can account for turtles' long-distance movements.

We examined the tracks of surface drifting buoys near loggerhead nesting beaches in the southeastern U.S. and the trajectories of virtual turtles released into two ocean circulation models to assess the probability of long-distance transport by passive drifters. We then simulated offshore swimming from the same locations to determine whether swimming influenced turtles' probability of survival, reaching distant foraging grounds, and encountering favourable temperatures. In this way, we address the more general questions of how natal site and animal behavior, acting in isolation and in synergy, influence the movement ecology and dispersal potential of marine organisms.

Methods

Study region

We examined likely dispersal scenarios for hatchling turtles from the main loggerhead nesting regions in the southeastern U.S. These regions included: North Carolina (NC); South Carolina (SC); Georgia (GA); northeastern Florida (from Cape Canaveral to the Georgia border) (NE FL); southeastern Florida (from Miami to Cape Canaveral) (SE FL); southwestern Florida (Pinellas to Monroe County) (SW FL); and northwestern Florida (from the Alabama border to Franklin County, Florida) (NW FL) (Putman *et al.* 2010a).

Assessment of ocean currents

The passive movement of virtual turtles (hereafter turtles) was simulated for 2 years using hindcast output from two ocean circulation models: Nucleus for European Modelling of the Ocean (NEMO) (Madec 2008) and Global Hybrid Coordinate Ocean Model (Global HYCOM) (Bleck 2002). Using ESRI ArcGIS, 250 randomly assigned points were selected 25–50 km offshore of each region to serve as the start location of simulated turtles. These locations bracket the 30–40 km estimate of the maximum distance turtles can travel during their frenzy period (Kraemer and Bennett 1981) to account for conditions (e.g., wind, waves, tides, etc.) that might increase or decrease the distance travelled by hatchlings. We tracked turtles from these seven nesting regions separately to examine variation in dispersal based on geographic differences in start locations.

Turtles were simulated in NEMO using the particle tracking program ARIANE to calculate surface trajectories of buoyant particles through an evolving model velocity field (http://stockage.univ-brest.fr/~grima/Ariane/). The version of NEMO featured in this study was developed at the National Oceanography Centre, Southampton. NEMO is forced with atmospheric conditions that combine 6-h air temperature, humidity, and wind fields from the ERA40 reanalysis with climatological radiation and freshwater fluxes from the CORE dataset (see Scott *et al.* 2012). The available velocity fields have a spatial resolution of 0.25° (c. 24 km grid spacing) that were averaged over 5 days. In this configuration, NEMO resolves the variability of energetic currents, such as the Gulf Stream, and oceanic eddies of radii exceeding around 100 km.

Turtles were simulated in Global HYCOM with the particle-tracking program ICHTHYOP v. 2.21 (Lett *et al.* 2008). For advection of particles, ICHTHYOP implemented a Runge–Kutta fourth-order time-stepping method whereby particle position was calculated hourly (Lett *et al.* 2008). Unlike earlier simulations using ICHTHYOP (e.g., Putman *et al.* 2010b, 2012), particles were not excluded from further analyses if they were advected into coastlines. Instead, particles were transported along the coastline in the direction of current flow until currents changed to move them offshore. Global HYCOM output has a spatial resolution of 0.08° (c. 7 km grid spacing), a daily time step, and is forced using wind stress, wind speed, heat flux, and precipitation. HYCOM assimilates satellite altimetry data, sea surface temperature, and in situ measurements from a global array of XBTs (expendable bathythermographs), ARGO floats, and moored buoys to produce realistic hindcast model output. Thus, Global HYCOM accurately resolves mesoscale processes such as meandering currents, fronts, filaments, and oceanic eddies (Bleck 2002; Chassignet *et al.* 2007). The study domain for our Global HYCOM simulations extended from the Equator to 47° N and from 100°W to the Prime Meridian.

Previous modelling studies on hatchling dispersal suggest that interseasonal and interannual variation in ocean current conditions can greatly influence the results of simulations (Putman *et al.* 2010b; Hays *et al.* 2010). We therefore released turtles at three times during the hatching season (the last day of July, August, and September) and tracked them for 2 years. The available output for NEMO extended from 2000 to 2006

and HYCOM output was available from 2004 to 2010. Thus, within each model, we tracked 5 turtle cohorts. In our analyses, we treat each of the 15 different release periods independently because of the unique oceanic conditions that existed during each release event.

Lagrangian drifter data were downloaded from the NOAA-AOML global drifter dataset to provide empirical data on ocean currents in the vicinity of nesting regions (http://www.aoml.noaa.gov/envids/gld/). All buoys passing between 25 and 50 km of the 7 nesting regions were selected. This resulted in a variable number of buoys obtained for each region (NC = 57, SC = 4, GA = 1, NEFL = 19, SEFL = 108, SWFL = 3, NWFL = 2). With the exception of the South Carolina region, mean initial locations of AOML buoys were systematically seaward (by several tens of km) of the release sites in our simulations. These data should therefore be interpreted with appropriate caution, in that they are likely to overestimate dispersal potential from sea turtle nesting beaches. To supplement this dataset, we obtained data from published studies that deployed surface drifters that passed in the vicinity of these regions (Ohlmann and Niiler 2005; Edwards *et al.* 2006; Hare and Walsh 2007). These publications provided data for 3 buoys from NC, 2 from SC, 26 from GA, 2 from NEFL, 20 from SEFL, 1 from SWFL, and 57 from NWFL. Sufficient information was not available to determine whether systematic biases (relative to our simulations) were present in drifter data obtained from the literature, and thus, results are reported separately from the NOAA-AOML drifters.

Differences among model output and buoy data were accounted for by using the findings to qualitatively bracket a range of scenarios for how ocean circulation is likely to influence long-distance transport in hatchling loggerheads. For simulations and empirical buoy data, we report the percentage of particles and buoys from each nesting region that remained over the continental shelf (water depth< 200 m) for more than 30 days. For NEMO and HYCOM simulations, we report the mean percentage of particles (and 95 % CI) as calculated from 15 different release events over a period of 5 years. For surface drifting buoys, we report the number of buoys that remained over the shelf for 30 days or ran aground divided by the total number of buoys per region. We also report the percentage of particles and buoys that travel east of longitude 30°W within 2 years. Results from NEMO and HYCOM are reported as before, whereas for buoys the percentage is calculated based on the number that cross this longitude within 2 years

divided by the total buoys that drift for at least a year plus the number of buoys that ground in Western Atlantic.

Simulating offshore swimming

The influence of additional offshore swimming on the subsequent movement of young turtles was modelled using simulations in which turtles swam for varying lengths of time during the ''post-frenzy'' week. Conservative estimates of swimming behavior were chosen to ensure that we did not overestimate the potential impact of turtle behaviour on their movement. We assumed that after reaching the points 25–50 km from the coastline, turtles engaged in 12 h of offshore swimming for 1–7 days (i.e. 12–84 total hours of swimming). This is a conservative estimate of physiological capacity given that post-frenzy hatchlings actively swim during daylight hours and occasionally during the night (Salmon and Wyneken 1987; Wyneken and Salmon 1992; Wyneken *et al.* 2008). Thus, for each of the 7 nesting regions, we have a total of 8 dispersal scenarios; one passive scenario and 7 in which swimming was simulated.

Although young loggerheads have been measured sustaining swimming speeds upwards of 0.2–0.4 $m.s^{-1}$ (O'Hara 1980; Salmon and Wyneken 1987; Witherington 1991), more conservative estimates were chosen (O'Hara 1980; Kraemer and Bennett 1981). Simulated turtles were programmed to randomly pick a speed between 0.15 and 0.20 $m.s^{-1}$ for each hour that they were active. This behaviour would result in turtles, on average, swimming 7.56 $km.d^{-1}$ in still water. The headings that turtles were programmed to adopt differed depending on region. Turtles from the eastern U.S. coast swam east and each hour they randomly chose headings within ± 20° of 90°. From the southwest coast of Florida, turtles swam west (270° ± 20°). From the panhandle of Florida, turtles swam south (180° ± 20°). Headings were chosen in accordance with the offshore direction and the approximate degree of scatter in field observations (Salmon and Wyneken 1987). We performed these simulations with the Global HYCOM output because modifications made to ICHTHYOP (v. 2.21) allowed us to seamlessly couple swimming behavior of simulated turtles to the Global HYCOM velocity fields (Putman *et al.* 2012). Additionally, the finer spatial and temporal resolution of Global HYCOM output (0.08° and daily), compared to available NEMO output (0.25° and 5 day mean), depicts small-scale oceanic features which are important in realistically characterizing dispersal scenarios of turtles and other small organisms (Witherington 2002; Cowen *et*

al. 2006). Simulations of offshore swimming followed the same releasing scheme as described above for modelling passive drift.

Estimating mortality and fitness metrics

The influence of oriented swimming from different nesting beaches on loggerheads was assessed by estimating turtle mortality based on body temperature and nearshore predation. As proxies, we determined the daily sea surface temperature (SST) and water depth encountered by turtles. SST has a strong influence on survival and growth in sea turtles (Davenport 1997). Water depth is correlated with predation risk, with highest risk over the continental shelf (< 200 m depth) where the density of predators for small turtles is relatively high (Carr 1987; Collard and Ogren 1990; Wyneken and Salmon 1992; Whelan and Wyneken 2007; Wyneken *et al.* 2008). We assumed that any turtle encountering SST < 10.0°C died and that a turtle experiencing a mean SST <15 °C for more than 10 days had a 50 % chance of dying (Davenport 1997). For predation, we assumed an individual turtle younger than 1 year had a 5 % chance of mortality each day in waters <100 m deep and 1 % chance of mortality between 100 and 200 m deep. Values of SST were based on output from Global HYCOM and bathymetry was from the Digital Bathymetric Grid Database (v.2), a project of the U.S. Naval Research Laboratory. After modelling mortality, we then calculated the likelihood of turtles reaching distant foraging grounds and encountering favourable SST. These metrics were defined as the number of turtles reaching the Azores (an important transatlantic foraging ground (Carr 1987)) and the number of turtles spending more than 50 % of the simulation in waters > 20 °C (temperatures that favour growth (Davenport 1997)).

Kruskal–Wallis tests determined whether natal region and offshore swimming influenced each metric of hatchling fitness (probability of survival, reaching appropriate nursery habitat, and encountering favourable temperatures). The Spearman Rank Correlation test was used to determine whether increased offshore swimming activity was correlated with the means of each fitness metric. For each nesting region pairwise Wilcoxon Signed Rank tests determined the amount of post-frenzy swimming required to influence fitness metrics.

For each natal region, linear regressions estimated the relationship (slope) between the amount of offshore swimming and the three fitness metrics to examine whether the

influence of offshore swimming was related to ocean circulation. The Spearman Rank Correlation test was performed using the slope of the regression line and its' intercept for each nesting region. A positive correlation between the slope and intercept would indicate that offshore swimming had a greater effect from nesting regions where currents were most favourable under the assumption of passive drift.

Results

Surface currents near loggerhead nesting beaches

Modelled and empirical scenarios of drift along the southeastern U.S. coast indicate differences in likelihood of retention and long-distance transport among the 7 loggerhead nesting regions. In general, the NEMO simulations, Global HYCOM simulations, and buoy data agreed that retention over the continental shelf was most likely for nesting regions in the Gulf of Mexico and South Atlantic Bight (Table 1). In contrast, passive objects were more likely to be advected offshore from Southeast Florida and North Carolina (Table 1). However, even in these regions, substantial numbers of drifters are likely to remain over the continental shelf for at least a month.

In oceanic waters, NEMO tended to predict that turtles would remain within the main jet of the Gulf Stream and be transported to the eastern Atlantic, whereas Global HYCOM predicts a higher degree of dispersion, consistent with the finer resolution and more energetic eddy field of that model (Fig. 1). This finding is consistent with others that have shown smaller-scale and higher-energy oceanic processes are likely responsible for reduced potential for dispersal. Even so, some agreement can be found between these models; simulated turtles from nesting regions of more northerly sites (North Carolina and South Carolina) had a greater likelihood of being transported east of longitude 30°W within 2 years than regions to the south (Table 2). Similarly, a relatively high percentage of buoys crossing east of longitude 30°W were from the North Carolina region.

Influence of offshore swimming on fitness metrics

Each scenario of swimming behavior revealed that simulated turtles from different nesting regions had significantly different likelihoods of survival, reaching the Azores, and encountering favourable SST (Kruskal–Wallis test, $H > 31.9$, $P < 1.7\ 10^{-5}$; for each scenario of swimming activity). In general, fitness metrics tended to be higher for

simulated turtles from beaches with a shorter cross-shelf distance to the open sea (e.g., Southeast Florida, North Carolina, and Northwest Florida) than those from beaches behind a wider portion of the shelf (e.g., Georgia, South Carolina, and Southwest Florida).

Increased swimming strongly correlated with an increase in each fitness metric for 6 of the 7 nesting regions (Spearman correlation test, $R > 0.898$, $P < 0.002$; for each natal site and for each fitness metric). There was no correlation between swimming activity and any fitness metric for turtles from Georgia (Spearman correlation test, $R < 0.095$, $P > 0.823$; for each). Thus, from most nesting regions, turtles appear capable of increasing fitness benefits under conservative estimates of offshore swimming. Wilcoxon Sign Rank tests comparing fitness metrics between simulations of passive drift and different amounts of offshore swimming revealed that, from some nesting regions, turtles could significantly alter the dispersal outcome assumed for passive drift with minimal swimming, whereas turtles migrating offshore from other regions would require more effort (Table 3).

Linear regressions of the amount of offshore swimming and the 2-year mean of the three fitness metrics for each level of swimming activity (Fig. 2) further suggest that even a modest amount of swimming was likely to have quantifiable fitness benefits for young turtles (Table 3). The slope of the regression lines for each nesting region was strongly correlated with the intercepts (where swimming activity is 0 hr) (Spearman correlation test, $R > 0.893$, $P < 0.025$; for each fitness metric). This implies that offshore swimming has the greatest positive influence on fitness from regions where oceanic conditions are already most favourable.

Discussion

Analyses of two different ocean circulation models and empirical data from surface drifting buoys indicate that the loggerhead nesting regions along the southeastern U.S. coast differ greatly in how well they promote or impede long-distance transport (Tables 1,2). This important role of location along the coast in relation to offshore currents is likely to apply equally to the many thousands of littoral animal and plant species that have planktonic stages. Our results suggest that population success and connectivity between populations will be profoundly influenced by the prevailing offshore ocean

currents. Additionally, simulations that incorporated offshore swimming behavior in a high-resolution ocean circulation model show that even moderate amounts of simulated offshore swimming confers fitness benefits for young turtles, increasing turtles' probability of survival, reaching distant foraging grounds, and encountering favourable SST (Table 3; Fig. 2).

Interestingly, when offshore swimming was simulated, loggerhead fitness increased much more at regions that were more favourable under scenarios assuming passive drift than regions that were less favourable. For instance, turtles modelled as passive drifters from Southeast Florida had higher probability of reaching distant foraging grounds in the Azores than regions in the South Atlantic Bight (Northeast Florida, Georgia, and South Carolina) and Gulf of Mexico (Southwest Florida and Northwest Florida), even when simulated turtles from these regions swam the maximum amount of time (Table 2; Fig. 2b). This implies that the location of nesting beaches from which hatchling loggerhead sea turtles disperse plays a central role in determining subsequent dispersal (and possibly survival) scenarios of young turtles. These differences in dispersal potential likely have profound ecological implications on the populations of turtles that nest in different regions (Wyneken *et al.* 2008). Indeed, the distance that hatchlings must travel before reaching the Gulf Stream System appears to be the main limiting factor in loggerhead nest density along the southeastern U.S. coast (from Texas to North Carolina) (Putman *et al.* 2010a). For other sea turtle species, including Kemp's ridley (*Lepidochelys kempii*) and leatherbacks (*Dermochelys coriacea*), beaches with high nest density are also in close proximity to ocean currents that promote offshore transport of hatchlings (Putman *et al.* 2010b; Shillinger *et al.* 2012).

Implicit in our present findings is that low survival of young turtles in coastal waters is a key driver in long distance, oceanic dispersal. Coastal areas are recognized as inappropriate habitat for young turtles due to intense predation that results from increased predator density relative to open ocean habitats (Carr 1987; Collard and Ogren 1990). Another important factor of mortality along temperate and subtropical coastlines is that temperatures in the surface waters can become fatally cold to turtles during winter (Collard and Ogren 1990). Thermal unsuitability of coastal waters, particularly in the South Atlantic Bight, is seen by modelling the mortality of passively drifting turtles based only on SST and comparing it to mortality based on both water

depth and SST (Fig. 3). Wintertime temperatures experienced by simulated turtles remaining in coastal waters could result in substantial mortality for turtles from many nesting regions. An additional line of evidence of this is that older turtles migrate hundreds of kilometres southward or into the open sea at the onset of cooler temperatures (Mansfield *et al.* 2009), a solution that young, weakly swimming turtles are not able to exploit.

If young turtles are to consistently achieve transport out of coastal areas and remain in oceanic waters, some level of sustained swimming is likely to be highly beneficial. This hypothesis and our present findings are corroborated by data obtained during an unusual oceanographic event in the summer of 2003. Due to a combination of strong winds that favoured upwelling and the Gulf Stream's position being more shoreward than is typical, relatively cold water intruded into the surface waters along the eastern U.S. continental shelf from c.27.5°N to c.35°N (Aretxabaleta *et al.* 2006; Hyun and He 2010). Hatchling turtles attempting to migrate offshore during this period became ''cold-stunned'' (incapable of swimming) and, as passive drifters, subsequently washed ashore along the east coast of Florida in record numbers (Loggerheadlines, June–July 2003, SC DNR; Aretxabaleta *et al.* 2006).

The oceanic constraint that is likely responsible for the retention of passively drifting objects along continental shelf of the southeastern U.S. is the system of oceanic frontal zones that delineate coastal and oceanic waters. Oceanic fronts are a consequence of the large-scale dynamical balance: a horizontal pressure gradient is established where water masses with different physical properties meet (Belkin *et al.* 2009). Due in part to Earth's rotation, the resulting frontal boundary becomes part of a geostrophic balance in which flow is directed along the front rather than across it. Loggerhead nesting beaches in the Gulf of Mexico are blocked by both the West Florida Shelf Front and the Loop Current Front; those on the Atlantic are blocked by the Mid-Shelf Front and/or the Inshore Gulf Stream Front (Belkin *et al.* 2009). On the shoreward side of these fronts, currents usually flow along the continental shelf and fronts typically act as barriers to offshore transport (He and Weisberg 2002, 2003; Ohlmann and Niiler 2005; Edwards *et al.* 2006).

Although cross-frontal exchange does occur as geostrophy breaks down at high current speeds in the presence of topographic obstacles (e.g. as the Gulf Stream flows past the "Charleston Bump" (Bane 1988)), it is not necessarily offshore. For instance, drifting objects initially entrained in the Gulf Stream System are frequently expelled along the southeast coast of Florida and into the South Atlantic Bight (Tester and Steidinger 1997; Yang *et al.* 1999; Hare *et al.* 2007). Seaward cross-frontal exchange is typically limited to a relatively narrow area of the eastern U.S. coast near Cape Hatteras, North Carolina (Savidge and Bane 2001). This, along with the initial release zone being seaward of the Mid-Shelf and the Inshore Gulf Stream Fronts, helps explain why the North Carolina region has relatively high fitness metrics for turtles (Table 3; Fig. 2). Even so, passive drifters transported north of Cape Hatteras by the Gulf Stream are routinely ejected shoreward into the Middle Atlantic Bight (Fig. 1; Hare *et al.* 2002).

Our findings have broad implications for understanding the movement of young turtles dispersing from coastal areas throughout the world. A global description of oceanic frontal systems (Belkin *et al.* 2009) shows that many loggerhead turtle nesting beaches are flanked by oceanic fronts associated with strong western boundary currents (e.g., along the southeastern U.S., east Australia, Japan, Brazil and South Africa). Loggerheads engaging in long-distance movements to the eastern Atlantic and eastern Pacific from these regions are certainly facilitated by the strong, nearby currents (Bowen *et al.* 1995; Boyle *et al.* 2009). However, our simulations suggest that turtles from many major nesting assemblages are likely to have difficulty moving beyond the frontal zones to the open ocean (and to the currents that promote transport) without sustained offshore swimming.

Moreover, recent modelling studies indicate that oriented swimming once in the open ocean also has important and favourable ecological consequences for young loggerheads (Putman *et al.* 2012; Scott *et al.* 2012). Indeed, it appears that navigation instructions encoded in subtle variations in earth's magnetic field are required for turtles to minimize the influence of small-scale processes that serve to eject passive drifters from the currents that facilitate transoceanic transport (Fig. 1; Putman *et al.* 2012). Thus, our examination of initial offshore swimming behavior provides compelling support for the emerging view that turtles and other marine organisms (e.g., Staaterman *et al.* 2012) benefit from taking an active role in their movements throughout life. This

is not to say that turtles swim continuously, or even very much, nor is this to say that modelling turtles as passive drifters for some purposes is without merit. Indeed, much can be learned about the oceanic constraints and factors shaping the ecology of sea turtles using such techniques (e.g., Blumenthal *et al.* 2009; Hays *et al.* 2010; Putman *et al.* 2010a). However, it is important to recognize that these small turtles, and other marine species that achieve long-distance transport, likely rely on strategies beyond passive drift and that even a minimal amount of swimming is likely to have an important function in their ecology and evolution.

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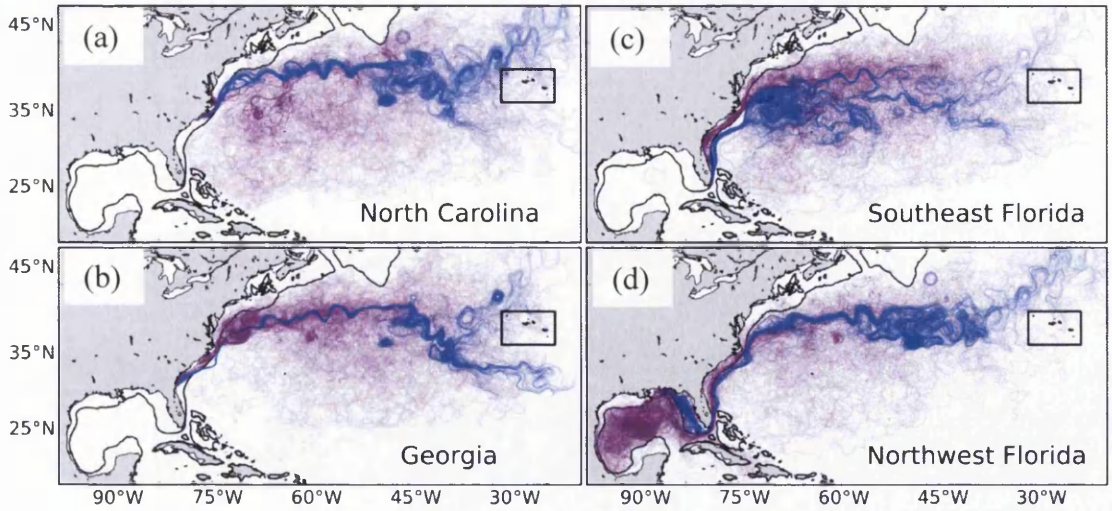

Fig. 1. Two-year trajectories of passively drifting particles released offshore of 4 loggerhead sea turtle nesting regions (a) North Carolina, (b) Georgia, (c) Southeast Florida, and (d) Northwest Florida. Shoreward of the single black line (parallel to the coast) indicates the continental shelf (water depth\200 m), where conditions are likely unsuitable for small sea turtles. The black rectangle surrounding the islands in the northeastern portion of the map indicates the Azores, an important foraging ground of young loggerheads from the southeastern U.S. Purple trajectories indicate the paths followed by 250 particles that were released into the global hybrid coordinate ocean model (HYCOM) starting at the end of August 2004. Blue trajectories indicate the paths taken by 250 particles released into the nucleus for European modelling of the ocean (NEMO) at the same time.

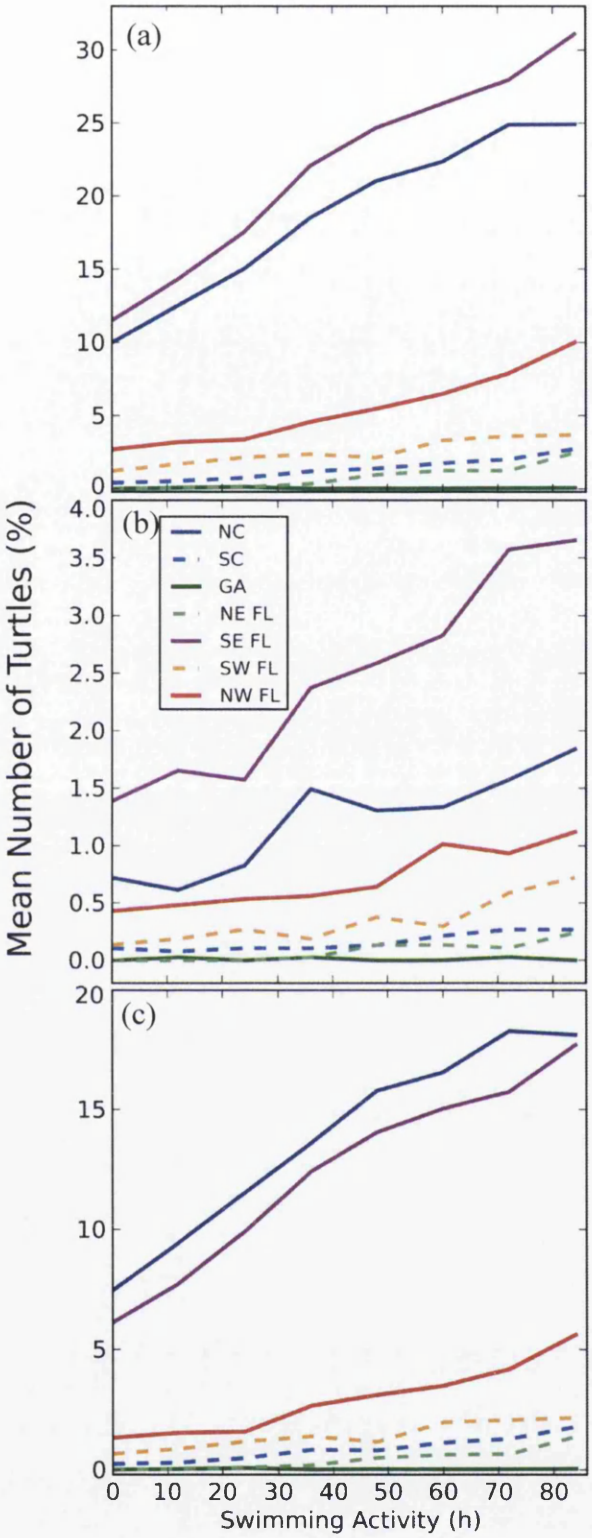

Fig. 2. The mean percentage of turtles that (a) survive, (b) reach the Azores, and (c) encounter favorable SST for a given amount of offshore swimming in the first 7 days of the simulation (note different scales along the y-axis for each). Each line represents the values for simulated turtles dispersing from a different nesting area (see inset box (b); the abbreviations of regions follow the conventions of Table 1).

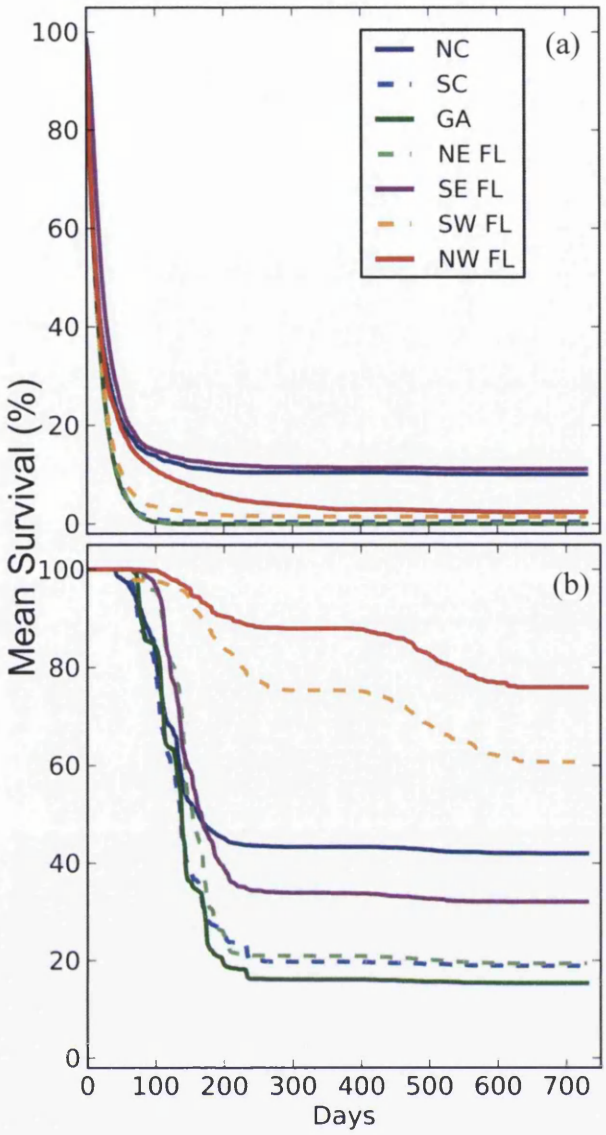

Fig. 3. Mean survival throughout 2 years (730 days) for behavioural scenarios assuming passive drift in the 15 HYCOM simulations. Turtle mortality was modelled based on (a) sea surface temperature (SST) and water depth and (b) SST alone. Each line represents the mean values for simulated turtles dispersing from a different nesting area (see inset box (a); the abbreviations of regions follow the conventions of Table 1).

Table 1. The percentage of particles and buoys from each nesting region that remain over the continental shelf (water depth < 200 m) for 30 days. The ratio of buoys used to calculate the percentage is in parentheses. For NEMO and HYCOM simulations, the 95 % CI of the mean is in parentheses. Region abbreviations are NC North Carolina, SC South Carolina, GA Georgia, NE FL northeast Florida, SE FL Southeast Florida, SW FL Southwest Florida, NW FL Northwest Florida ([a] Hare and Walsh 2007; [b] Edwards *et al.* 2006; [c] Ohlmann and Niiler 2005).

Region	AOML Buoys	Other Buoys	NEMO	HYCOM
NC	9.1	66.7[a]	14.1	65.0
	(4/44)	(2/3)	(8.5)	(13.6)
SC	100.0	100.0a	24.4	98.7
	(4/4)	(2/2)	(11.5)	(1.4)
GA	100.0	100.0[ab]	46.3	100.0
	(1/1)	(26/26)	(22.5)	(0.0)
NE FL	50.0	100.0[a]	46.7	100.0
	(9/18)	(2/2)	(20.0)	(0.0)
SE FL	30.2	50.0[a]	9.7	78.2
	(16/53)	(10/20)	(5.0)	(11.3)
SW FL	100.0	100.0a	56.6	95.8
	(3/3)	(1/1)	(19.3)	(7.9)
NW FL	100.0	91.2[c]	89.9	75.3
	(2/2)	(52/57)	(6.5)	(13.3)

Table 2. The percentage of particles and buoys from each nesting region that cross into the eastern Atlantic, as defined by longitude 30°W. Region abbreviations and other conventions follow those in Table 1.

Region	AOML Buoys	NEMO	HYCOM
NC	82.1 (23/28)	60.5 (12.4)	19.6 (3.4)
SC	0.0 (0/2)	58.3 (15.5)	17.4 (3.5)
GA	0.0 (0/1)	49.0 (15.68)	10.5 (3.0)
NE FL	88.9 (8/9)	50.4 (12.1)	10.4 (1.9)
SE FL	32.5 (14/43)	20.7 (6.9)	15.3 (2.6)
SW FL	0.0 (0/1)	24.5 (8.6)	7.8 (2.3)
NW FL	NA	15.2 (7.0)	4.3 (1.6)

Table 3. The influence of offshore swimming on three metrics of sea turtle fitness. Region abbreviations follow conventions of Table 1. Spearman's r ("R"), larger values indicate a positive relationship between swimming activity and fitness metrics. The p value is in parentheses beneath. "B" is the intercept of the linear regression and shows the value of the fitness metric when there is no offshore swimming. The slope of the regression "M" is in parentheses beneath. "Hrs" indicates the number of hours turtles swam in the simulation before a Wilcoxon Sign Rank test detected a difference ($P < 0.05$) in fitness between that simulation and the one assuming passive drift.

Regions	Survival			Transport to Azores			Favorable SST		
	R (P)	B (M)	Hrs	R (P)	B (M)	Hrs	R (P)	B (M)	Hrs
NC	1.0 (< 0.01)	10.7 (0.19)	12	0.90 (< 0.01)	0.63 (0.013)	36	0.98 (< 0.01)	8.2 (0.14)	12
SC	1.0 (< 0.01)	0.3 (0.03)	24	0.92 (< 0.01)	0.06 (0.002)	60	0.98 (< 0.01)	0.1 (0.02)	36
GA	0.03 (> 0.5)	0.1 (0.00)	>84	0.10 (> 0.5)	0.01 (0.000)	>84	-0.07 (> 0.5)	0.0 (0.00)	>84
NE FL	0.98 (< 0.01)	-0.3 (0.03)	24	0.90 (< 0.01)	-0.03 (0.003)	48	1.0 (< 0.01)	-0.2 (0.01)	48
SE FL	1.0 (< 0.01)	12.2 (0.23)	12	0.98 (< 0.01)	1.22 (0.029)	48	1.0 (< 0.01)	6.6 (0.14)	12
SW FL	0.93 (< 0.01)	1.3 (0.03)	36	0.90 (< 0.01)	0.07 (0.006)	72	0.93 (< 0.01)	0.7 (0.02)	60
NW FL	1.0 (< 0.01)	1.9 (0.08)	12	0.98 (< 0.01)	0.35 (0.009)	48	1.0 (< 0.01)	0.9 (0.05)	48

Chapter 4

Lost at sea: genetic, oceanographic and meteorological evidence for storm-forced dispersal

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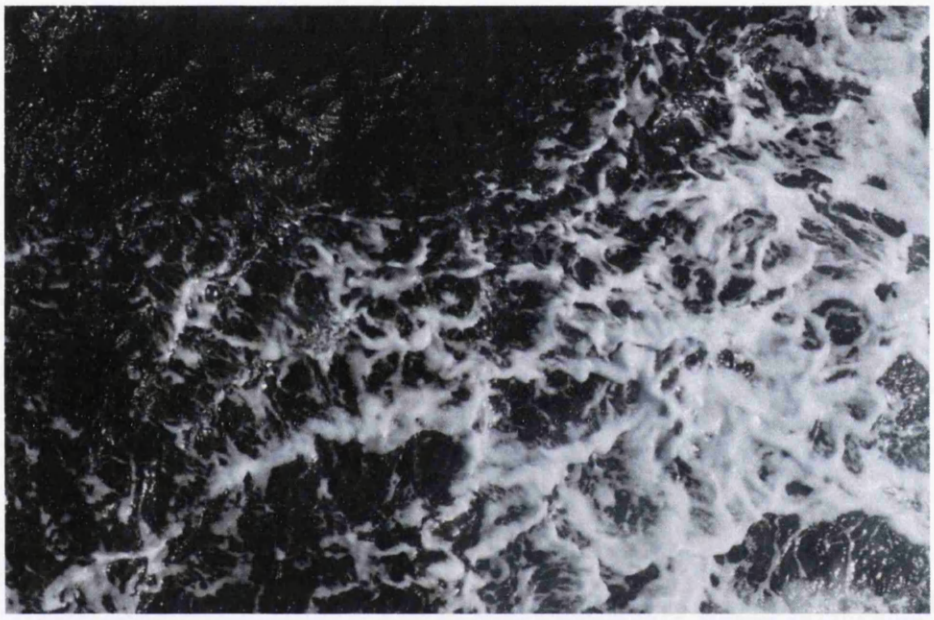

Disclaimer: RS compiled and analysed all the Lagrangian surface drifter buoy data. RM set up the ocean model so that RS could compute and analyse the 11,820 3-year long ocean model hindcast trajectories. RS prepared figure 3. CM-A and PLML conceived the study, analysed the genetic data and wrote the paper together, with contributions from all other authors. RS, RM and GCH provided oceanographic and meteorological contributions. FD'A, PM, AM, LFL-J provided samples and laboratory resources.

Abstract

For many species there is broad scale dispersal of juvenile stages and/or long–distance migration of individuals and hence the processes that drive these various wide-ranging movements have important life-history consequences. Sea turtles are one of these paradigmatic long-distance travellers, with hatchlings thought to be dispersed by ocean currents and adults often shuttling between distant breeding and foraging grounds. Here, we use multi-disciplinary oceanographic, atmospheric and genetic mixed stock analyses to show that juvenile turtles are encountered 'downstream' at sites predicted by currents. However, in some cases, unusual occurrences of juveniles are more readily explained by storm events and we show that juvenile turtles may be displaced 1000s of km from their expected dispersal based on prevailing ocean currents. As such, storms may be a route by which unexpected areas are encountered by juveniles which may in turn shape adult migrations. Increased stormy weather predicted under climate change scenarios suggest an increasing role of storms in dispersal of sea turtles and other marine groups with life-stages near the ocean surface.

Introduction

Long distance migration remains one of nature's wonders. Migratory animals exploit different locations at different stages in their life: a strategy so effective at optimising resource use that the cost of travel is worthwhile (Alexender 1998). The iconic questions of where eels go to spawn (Avise 2011), and how sea turtles and salmonids navigate and the factors that shape their migratory routes (Lohmann *et al.* 2008; Byrne *et al.* 2009; Sale *et al.* 2009) continue to drive scientific investigation. These studies go beyond curiosity, as anthropogenic changes to the environment are affecting large-scale processes (e.g. climate) that may have consequences for migratory behaviour and species survival (Wilcove and Wikelski 2008). It is therefore suggested that global migrators, such as transoceanic migratory birds, may be useful as biological indicators of climate and oceanic health (Shaffer 2006).

For aerial organisms, global wind patterns are a strong determinant of long-distance migratory routes (Felicísimo *et al.* 2008), but in the sea, it is the prevailing oceanographic features, such as circulation patterns, that are believed to be important in determining the distribution and connectivity of populations. Many species have been shown to use ocean currents as migratory pathways. For juvenile stages of marine organisms, small size may limit their capability to swim actively against currents, so 'going with the flow' would be an efficient means of migrating to distant foraging grounds while maximising growth and development. For example, in the North Atlantic, the 'subpolar gyre' is used by Atlantic salmon (Dadswell 2010) and the 'subtropical gyre' is used by sea turtles (Luschi *et al.* 2003).

These gyres are major currents that occur at the ocean basin scale. At this scale in the subtropics, the 'subtropical gyre' is set up by the 'Sverdrup transport' (Sverdrup 1947), which is a broad equatorward flow across the subtropics. Northward return flow in the gyre is confined to a western boundary region, governed by frictional processes (Stommel 1948; Munk 1950), and is consequently swift. These return flows comprise the ocean currents of leading importance for the long-distance migration of marine organisms. Such currents are quasi-steady, subject to some seasonality, particularly in wind forcing, e.g., (Niller *et al.* 1973) and dynamical instability (eddying). Current speeds are typically in the range of 10-100 $cm.s^{-1}$. Current width ranges considerably, from narrow swift flows spanning a few km (e.g. the Florida Current) to broad weak

flows spanning several hundred km (e.g. the North Atlantic Current). Moving into mid-latitudes, some boundary currents (e.g. the Slope Current at the northwest European shelf break (Huthance 1995)) are principally driven by surface buoyancy forcing, due to the combined effects of heat and freshwater exchange between ocean and atmosphere. In addition to the balanced upper circulation, surface 'Ekman Currents' arise through a balance between frictional forces associated with the wind and the Coriolis force, with the surface current oriented 45° to the right of the wind in the northern hemisphere (Ekman 1905). Ekman Currents are most conspicuous in the 'interior' of the subtropical gyre, where the upper circulation is weak. Buoyant objects in the ocean, such as drifting organisms, thus move under the combined influence of quasi-steady and Ekman Currents.

Although major migratory pathways of marine organisms appear to be fixed by ocean currents, frequent reports of 'stranded' or 'vagrant' individuals outside their ranges are common for many species including seals (Ferreira *et al.* 2008), cetaceans (Leeney *et al.* 2008) and sea turtles (Hart *et al.* 2006), indicating that animals can be displaced from normal migratory routes. Occasionally, displacement events are dramatic: for example the 1000s of km displacement of an Emperor penguin this year (http://www.bbc.co.uk/news/world-asia-pacific-13856024). Such dramatic displacements are rare, but in some locations, strandings of marine vertebrates are routine (Hart *et al.* 2006; Leeney *et al.* 2008), and present opportunities to investigate whether there are factors other than currents that may influence dispersal.

Here we focus on sea turtles, one of the paradigmatic long-distance migrators (Hays *et al.* 2003). Adult turtles return to natal nesting beaches to breed and some species maintain fidelity to specific foraging grounds that may be 1000s of km from the breeding sites (Avise 2007; Bowen *et al.* 2007). Our focal species, the loggerhead sea turtle (*Caretta caretta*), is one of the most well-studied of sea turtle species. After emerging from nests, hatchling loggerhead sea turtles enter the sea and the juveniles then spend several years in the open ocean, followed by a transition from pelagic to neritic habitats when individuals are around 40-50 cm in size (Bowen *et al.* 2005), although exceptions to this general life cycle have been found (McClellan *et al.* 2010). Pelagic juveniles are therefore of relatively small size, and still subject to any oceanographic and meteorological forces that may alter their direction of dispersal in

the open seas. In the North Atlantic, it is known that loggerhead juveniles spend 6.5–11.5 years within the oceanic zone (Bjorndal *et al.* 2000). These either remain around the American mainland, or are transported in the North Atlantic subtropical gyre towards the eastern Atlantic, where there are major foraging grounds for juvenile turtles, for example, around the Azores and the Canary Islands (Monzón-Argüello *et al.* 2009). The trans-Atlantic drift from eastern USA to Europe is estimated to be 1.80–3.75 years (Hays *et al.* 1997). Those transported further north from the normal foraging grounds towards Northern Europe by the North Atlantic Current, may die from cold stunning (Witt *et al.* 2007). Sea turtles are known to orientate in order to nest in their natal beaches and reach specific feeding areas (Lohmann *et al.* 2008). This orientation is based, at least partly, on geomagnetic cues and may help loggerhead sea turtles to remain in warm waters (Lohmann *et al.* 2008). However, when currents are strong or during extreme weather events, this ability may be reduced because of the limited swimming strength of juveniles that are small in size (Revelles *et al.* 2007; Monzón-Argüello *et al.* 2009), particularly as they start to become cold stunned. Individuals failing to correct their drift might end up stranded far north of their normal foraging grounds, for example in areas of Northern Europe such as the Bay of Biscay or the English Channel.

We examine mitochondrial DNA (mtDNA) sequences of juvenile loggerhead sea turtles (*Caretta caretta*) stranding around the Bay of Biscay to estimate the origins of these turtles. The study area lies outside of the species' normal range, with the nearest foraging areas in the Azores and southern Spain. These stranded juvenile loggerhead turtles may have been transported by prevailing ocean surface currents, or they may have been blown off-course by storms. The episodic passage of cyclonic storms can influence the subtropical gyre of the North Atlantic. The passage of such storms will excite a dynamical response of the upper ocean in the form of Ekman Currents (Shay 2001). While the steady Ekman response to wind forcing (Ekman 1905) is not easily observed in the ocean, divergent Ekman Currents of 1-2 $m.s^{-1}$ have been observed in the wake of hurricanes, weakening over a few days (Shay 2001). A degree of asymmetry in the currents, along and about the axis of the hurricane, depends on the storm trajectory. A pattern of residual surface currents may thus be associated with cyclonic storms moving clockwise around the North Atlantic.

Classically, storms are well-known to cause unusual transport of terrestrial animals (Gressitt 1960). However, given that climate change models predict increasing storm activity (Webster *et al.* 2005), there is growing interest in understanding how storms impact on the dispersal and distribution of marine organisms (Lopez-Victoria and Zea 2004; Lea *et al.* 2009). In this study, we aim to consider both ocean currents and storm effects in understanding the factors driving the strandings of loggerhead turtles. Previous studies have found oceanographic data invaluable in interpreting the ecological and genetic structure of sea turtles (Hays *et al.* 2010; Godley *et al.* 2010; Monzón-Argüello *et al.* 2010; Okuyama *et al.* 2011), but in this study we take the multi-disciplinary approach a stage further in using oceanographic modelling as well as oceanographic and meteorological data in understanding the movements of sea turtles inferred from genetic data.

Methods

Genetic analyses

A total of 89 juveniles stranded in the Bay of Biscay from 1995 to 2009 were analysed (Fig. 1). Blood samples or tissue samples from skin or pectoral muscle were taken and stored in 96% ethanol at 4°C. Genomic DNA was isolated using DNeasy Tissue Kit (QIAGEN®) and a 760 base pair (bp) fragment of the mtDNA control region was sequenced using established primers and protocols (Abreu-Grobois *et al.* 2006). New haplotype sequences were submitted to the Archie Carr Center for Sea Turtle Research (http://accstr.ufl.edu/cclongmtdna.html) and GenBank. Arlequin version 3.0 (Excoffier *et al.* 2005) was used to estimate haplotype (h) and nucleotide diversity (π), and to perform exact tests of population differentiation (spatial and temporal genetic structure). We added unpublished sequences for the Cape Verde and Canary Islands in Bayesian 'many-to-many' mixed stock analysis (MSA) (Bolker *et al.* 2007; Spiegelhalter *et al.* 2010; Tables S1–S2 in Appendix 4).

We attempt to group individuals according to estimated origins. Haplotypes described for the Cape Verde population (Monzón-Argüello *et al.* 2010) were used to assign individuals to 'Cape Verdean' or 'American' groups. Haplotypes of uncertain assignment were excluded. Although not all individuals can be assigned and some errors could be introduced with this classification, it is a useful undertaking as it allows testing for differences between the two groups. We tested for size and weight variation

using the non-parametric Mann-Whitney U-test (SPSS 15.0), and for temporal variation using the G-test of independence.

Particle track modelling

To evaluate whether hatchlings leaving the Cape Verde Islands might passively drift to the broader Bay of Biscay region, we use both satellite-tracked buoy data (see next section) and model-based trajectories. In this section, we describe the latter. The ocean model, for which we diagnose trajectories of passively-drifting particles arriving in the Bay of Biscay, is based on NEMO (the Nucleus for European Modelling of the Ocean). We use fields from a global 1/4° implementation (Grist *et al.* 2010) that resolve the mesoscale variability of energetic currents and oceanic eddies of radii exceeding around 100 km. An efficient analytical method for computing large ensembles of offline trajectories (Blank *et al.* 2001) was customized as the ARIANE software (http://stockage.univ-brest.fr/~grima/Ariane/) for use with NEMO datasets. We specified particle 'end-points' in a regular grid spanning the Bay of Biscay (Fig. S1 in Appendix 4). To cover the period during which the sampled turtles are likely to have been at sea and to account for interannual variability, a particle is back-tracked from each end-point to obtain trajectory ensembles for the 3 years preceding 1995, 1998, 2001, 2004 and 2007. The trajectories are based on time-varying currents and are characterized by age (since release), depth (whether or not the particles are buoyant) and property (temperature and salinity). The spacing between adjacent end points was around 50 km. The end date for trajectories was mid-February of a selected year. Particles were constrained to remain at the uppermost NEMO depth level of 0.5 m, to mimic animal buoyancy. Advected by a surface velocity field that is updated every 30 days (as a monthly-mean field), a particle is back-tracked from each end point for 3 years or less (depending whether the particle originated from beyond the North Atlantic domain within 3 years). Positions of particles and associated water temperature are recorded every 5 days.

Lagrangian drifter and storm track data

To investigate the destination of turtles drifting away from the Cape Verde Islands, Lagrangian drifter data were downloaded from the NOAA-AOML global drifter program (http://www.aoml.noaa.gov/envids/gld/) with no restrictions on date or drogue attachment imposed. This dataset contains quality controlled data of over 14,500

satellite tracked surface buoys deployed since the 1970s. Buoys are drogued at 15 m (i.e. a sub-surface sea anchor, a "drogue", is tethered to the surface buoy) to reduce wind effects and interpolated to provide fixes at 6-hour intervals (Lumpkin and Pazos 2006). All buoys passing within 100 km of the coast of the Cape Verde Islands were selected, and upon first reaching this proximity, all subsequent fixes were used to investigate surface currents in this region.

Particle and buoy trajectories do not capture the influence of storm-induced displacement. While NEMO is forced by high-frequency winds, the particle trajectories are computed with monthly-averaged currents, and so storm-forced drift on timescales of hours-days is not explicitly included. Furthermore, the sampled buoys may not capture the relatively infrequent storm-induced drift, and being drogued to reduce wind effects, they will not experience the storm-induced fate of juveniles confined to the upper few meters. So to investigate storm trajectories, the tracks of major storms originating near Cape Verde Islands during our studied period were obtained from the National Hurricane Center website (http://www.nhc.noaa.gov/). This database is generated through the analyses of a wide variety of data, including the storm's life cycle (defined to include the tropical or subtropical depression stage, but does not include the extratropical stage) and maximum sustained (1-min average) surface (10 m) winds. For storms east of 55° W, the primary source of information was geostationary weather satellite imagery, with occasional *in situ* observations from ships and buoys. Only major storms (i.e. wind speeds of at least 17 $m.s^{-1}$) of the following classes were included in our data: 'tropical storm' with wind speed 17-32 $m.s^{-1}$; 'hurricane', wind speed 33-49 $m.s^{-1}$; 'major hurricane' with wind speed 50 $m.s^{-1}$ or higher. We use the term 'storm' generically to refer to all classes.

Results

Genetic analyses

Our data included 13 previously described, and two novel haplotypes (CC-A63.1 and CC-A64.1; GenBank accession numbers JF957336 and JF957337 respectively; Table S3 in Appendix 4). Using a short version of haplotypes (380 bp), pairwise comparisons between the stranded group and rookeries revealed significant differences (exact $P < 0.011$) except for Lebanon (exact $P = 0.149$), which has a small sample size ($n = 9$). Foraging ground centric MSA with population sizes as prior information (Table 1)

showed that a high proportion of juveniles were from the South Florida population (51%; 95% CI = 0.67), but surprisingly, juveniles from Cape Verde, in the eastern Atlantic, were relatively frequent (26%; 95% CI = 0.40) and more abundant than juveniles from northeast (8%; 95% CI = 0.19) or northwest Florida (1%; 95% CI = 0.03). There was no correlation with geographic distance to the Gulf Stream using either foraging ground centric ($R = 0.443$, $R^2 = 0.197$, $P = 0.098$) or rookery-centric MSA results ($R = 0.398$, $R^2 = 0.158$, $P = 0.329$).

The global test of population differentiation did not reveal genetic structure among the stranded group and foraging groups of the eastern Atlantic (exact P = 0.135). The stranded samples presented the highest h value (0.7043), but similar π (0.0342) to those of eastern Atlantic foraging grounds (Table S4 in Appendix 4). There were significant genetic differences among years (exact P = 0.001; Table S5-S6 in Appendix 4) but removal of 2001 data resulted in non-significance (exact P = 0.255). The greatest number of strandings occurred in 2001 and with a higher proportion of haplotype CC-A1.1 (0.40) than for other years (0.09-0.33). The number of strandings increased from December onwards with the highest proportion occurring in April (Fig. 2a) is consistent with other reports (Witt *et al.* 2007), and coincides with the months with lower sea surface temperature. Intra-annual genetic variation was detected for months with 5 or more samples (n= 8; exact P = 0.005).

The 'Cape Verdean group' (haplotypes CC-A1.3 and CC-A17.1; n=17) presented a higher proportion of dead animals (84%) than the 'American group' (29%; haplotypes CC-A1.1, CC-A3.1 and CC-A10.1; n =30) ($P < 0.001$; Table S3 in Appendix 4) but were not significantly different in size (n = 46, P = 0.767) or weight (P = 0.617). There were no genetic differences among months (n = 41, P = 0.299), but the critical months for strandings appear to be different (Fig. 2b). Additional differences could be observed in the stranding frequencies by year (n = 41, P = 0.021; Fig. 2c). 'Cape Verdean' individuals did not strand in every year that 'American' individuals stranded. For example, in 2001, the year with highest strandings, there were no 'Cape Verdean' individuals.

Analyses of physical data

A total of 11,820 3-year long Lagrangian hindcast trajectories were computed comprising a total of 2,588,580 particle locations. The general pattern of trajectories reflected the currents in this region: particles travelling to the Bay of Biscay would have originated from westwards in the North Atlantic Current after having streamed south/north in either the Labrador Current or Gulf Stream respectively (Fig. 3a). The majority of particles originated from the south near the southeast USA, Gulf of Mexico, Caribbean and Sargasso Sea. After 3 years of drift, particles were still only tracked back as far as the western Atlantic, and no particles originated close to the Cape Verde Islands.

All 53 buoys that were found to pass within 100 km of the Cape Verde Islands drifted westwards in the North Atlantic Gyre with the North Equatorial Current, bar one which drifted south towards the coast of Brazil before looping back towards the Cape Verde Islands (Fig. 3b). The buoy that had travelled the furthest reached a longitude of circa 60° west and 30° north within 3 years, which corresponded to locations where particles back-tracked from the Bay of Biscay reached in 2-3 years.

Eleven major storms originated near the Cape Verde Islands during our study period (Fig. 3c; Table S7 in Appendix 4). Several occurred during the nesting and hatching season of loggerhead turtles at Cape Verde (Varo 2010). These major storms initially travelled north-westwards from the Cape Verde Islands, but then travelled northwards and north eastwards to arrive in the northeast Atlantic.

Discussion

Here, we show that in addition to sea currents, storm-forcing may also impact on juvenile dispersion. The general importance of this is that it shows how stochastic weather effects may lead to drifting organisms arriving in areas that would not be predicted by dispersion on ocean current alone. Increasingly, studies of various organisms, ranging from rock lobsters (Chiswell *et al.* 2003) to kelp (Collins *et al.* 2010), are showing that many factors aside from prevailing oceanographic conditions may influence dispersal trajectories.

A general hypothesis of oceanic transport with major currents would predict that the stranded turtles in the Bay of Biscay should all come from rookeries along the coasts of the American continent. It has been suggested that proximity to the Gulf Stream may be important (Putman *et al.* 2010), but we found no such association for the stranded turtles. MSA showed that the Atlantic nesting populations were indeed the main contributors with half of all individuals from South Florida. The more interesting result, however, was that a quarter of stranded turtles were apparently from the Cape Verde Islands, which is nowhere near currents that would take hatchlings to the Bay of Biscay. The analyses of particle and buoy trajectories demonstrated that juveniles from the northwestern Atlantic, but not from Cape Verde, could arrive at the Bay of Biscay in a few years by drifting with ocean currents.

We consider here the influence of storm-driven surface currents on juvenile sea turtles, and suggest that storms may move turtles into other current systems that deliver them to locations outside their expected distribution and where they eventually stranded. During our study period, we identified 11 storms that could potentially influence the drift of juveniles from Cape Verde (Fig. 3). Interestingly, most of these storms occur around August-October (Table S7 in Appendix 4), while the highest frequency of strandings of Cape Verdean loggerheads occur in February (Fig. 2). It should be noted that the database we used was designed for tracking major storms, and there will be many more less-intense storms that may similarly be influencing the trajectory of hatchling turtles. However, the storms we identified provide evidence of the general predominant trajectories of storms in the Atlantic. Essentially, the predominant trajectory of storms provided a far more direct route from Cape Verde to the northeast Atlantic than that provided by prevailing ocean currents. Consequently, objects near the ocean surface moved by these storm winds would arrive in the northeast Atlantic much faster than objects carried by the current (Fig. 3). During the early stages, juveniles spend long periods at the ocean surface and storms could perhaps displace them sufficiently to end up on aberrant routes of migration. We suggest that juveniles would experience north westward drift in the vicinity of storms translating to the west in the tropics (10-25°N). If these juveniles move into the mid-gyre region (25-35°N), northward-translating storms will drive a north eastward drift. While these storm-induced 'nudges' are sporadic in nature (1-4 per year; Table S7 in Appendix 4) and short-lived, they are individually strong, and against a weak background flow of a few $cm.s^{-1}$, the net effect

on trajectories may be substantial. Driven sufficiently far to the north, juveniles will drift with the North Atlantic Current towards the Bay of Biscay (implicit in Fig. 3a). Subsequent entrainment in the Slope Current, flowing polewards along the shelf break, may account for the distribution of strandings evident in Fig. 1.

Displacement by storms could explain the difference in survival and the more irregular occurrences of strandings for the Cape Verde turtles. These did not strand every year, even though loggerhead turtles are stranded in the Bay of Biscay regularly. For example, in 2001, there was an unusually high rate of loggerhead turtles stranding in Europe (Bellido *et al.* 2008), but there were none in our data from Cape Verde. This would be consistent with stochastic events such as storms leading to a more irregular pattern of Cape Verde turtles reaching the Bay of Biscay.

Using multiple lines of evidence, we arrive at the conclusion that the loggerhead turtles that strand in the Bay of Biscay not only have different origins, but that their transport must have been driven by different factors. Prevailing oceanographic forces are thought to predominantly drive the direction of the dispersal of drifting organisms (Fraser *et al.* 2011). However, we show here that storm-forcing may perturb these regular patterns and although this may lead to novel dispersal or migration patterns, many individuals are also 'lost at sea' as a result. In our case, the turtles arrived in a sub-optimum area where cold temperatures can lead to death (Hays and Marsh 1997; Witt *et al.* 2007; Dell'Amico and Morinière 2010), but in other cases, we might expect the turtles could be blown to more favourable areas. Recently, it has been shown that variation in climate can influence the trajectory of storms in the Atlantic (Kossin *et al.* 2010; Wang *et al.* 2011). So if climate does change in the future, then the pattern of storm-forced dispersal may also change due to alterations to the overall directions of storms. Given that global warming models predict future increase in storm activity (Webster *et al.* 2005), we suggest that storm-forced dispersal will increase in importance, particularly for marine organisms with dispersive life-stages at the ocean surface.

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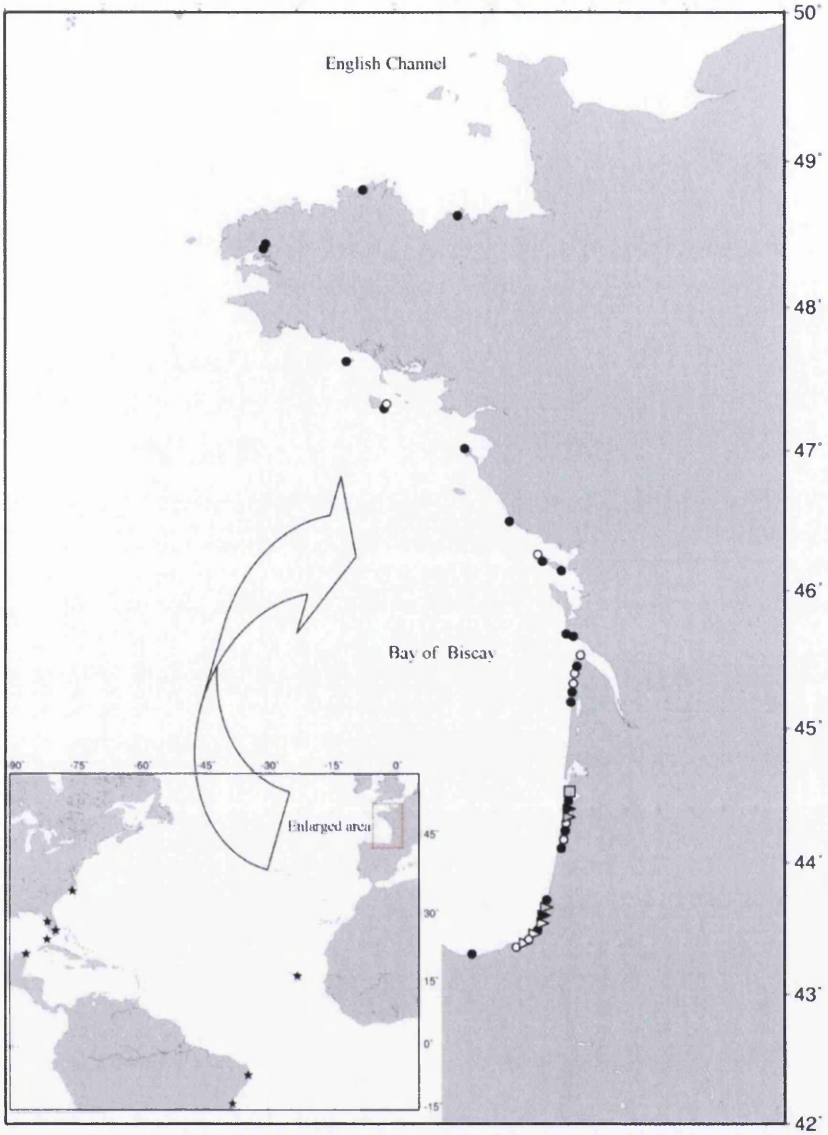

Fig. 1. Stranding locations of the individuals sampled in this study. Single strandings are represented by black circles; strandings of two, three, four, five and six individuals are represented by white circles, white triangles, grey triangles, black triangles and black squares respectively. The inset map shows the location of loggerhead nesting populations in the Atlantic (stars).

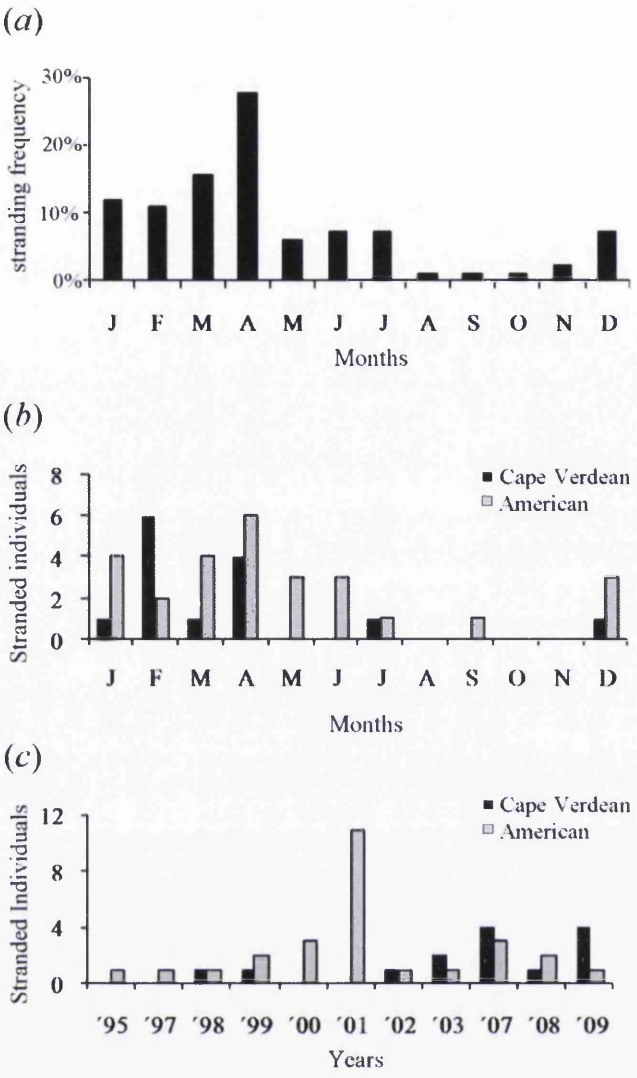

Fig. 2. Temporal distribution of strandings of loggerhead sea turtle juveniles off the Bay of Biscay. (a) The monthly distribution of all 82 stranding records (black) between 1995 and 2009 showed the highest frequency occurring in April. Months are ordered as in the calendar, and coded with the first letter of the month (i.e., starting with J = January, and ending with D = December). (b) The monthly distribution of 14 Cape Verdean (black) and 27 American (grey) individuals studied during this period. The critical months for strandings in the Bay of Biscay appeared to be different for turtles of different origins. (c) The distribution of 14 Cape Verdean (black) and 27 American (grey) individuals across the years included in the study (excludes years for which data were not taken). The distribution was significantly different for turtles of different origins (n =41, P = 0.021). Whereas individuals of American origin stranded in all the years studied, individuals from Cape Verde only stranded in some years. The high number of strandings that occurred during 2001 was all of American origin.

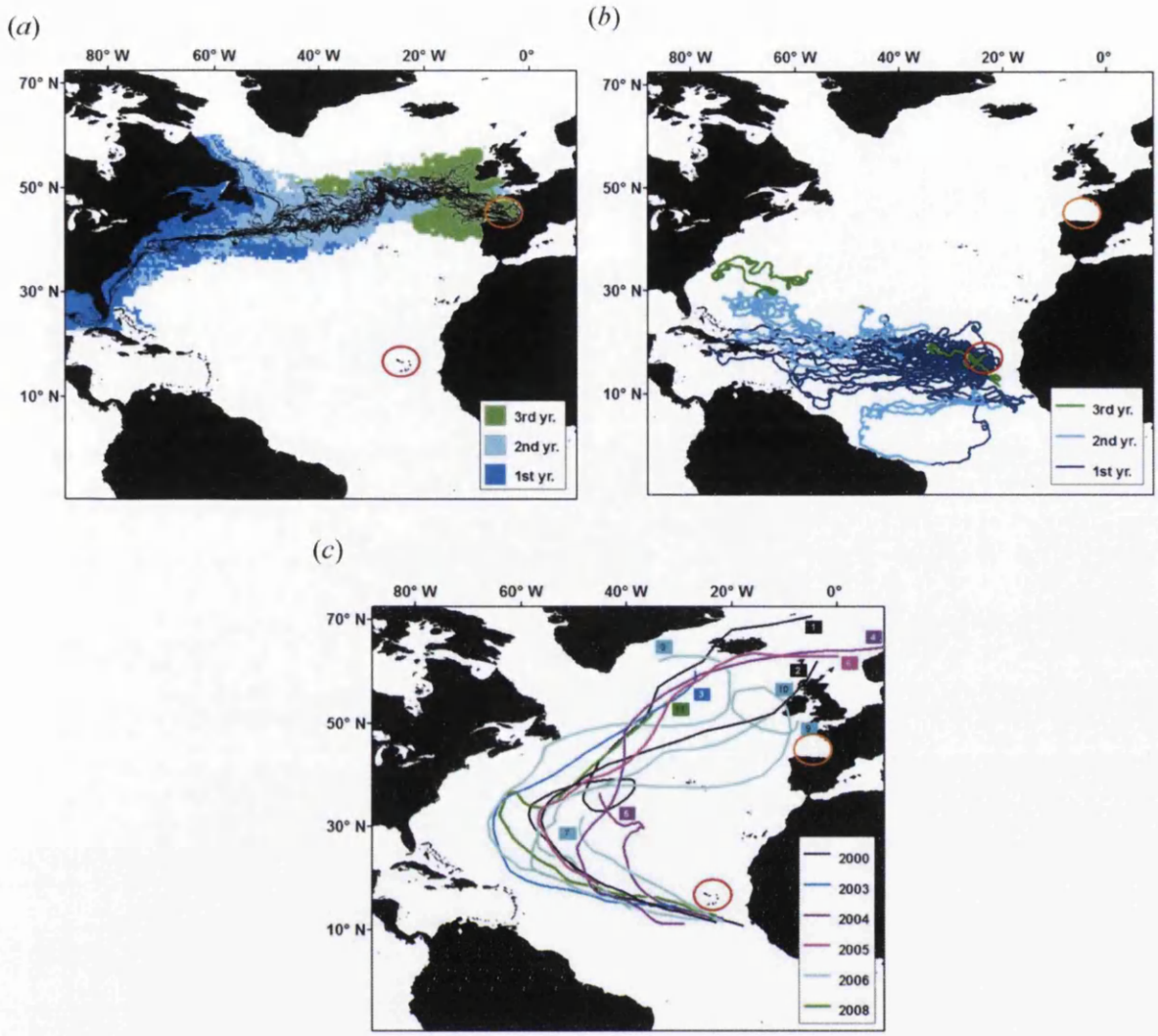

Fig. 3. Analysis of oceanographic and meteorological data for the North Atlantic to trace surface movements around Northern Europe/the Bay of Biscay (orange circle) and the Cape Verde Islands (red circle). (a) Mean drift time in each 0.5° by 0.5° pixel from the full particle hindcast ensemble. Pixels are coloured to reflect the first (dark blue), second (light blue) and third year of drift (green) and the paths of a sample of 35 particle hindcast trajectories are plotted. (b) Trajectories of 53 Lagrangian drifter buoys passing within 100 km off the coast of the Cape Verde islands. Pixels are coded as in (a) to reflect mean year of drift. (c) Tracks of eleven Atlantic basin major storms originated near Cape Verde Islands during our studied period. These storms provided a more direct route from Cape Verde Islands to the NE Atlantic than the prevailing ocean currents. Each color represents a different year. Further information about each storm numbered 1-11 is in Table S7 (Appendix 4).

Table 1. Mixed Stock Analysis (MSA) using 'many-to-many' model. The proportion of stranded juveniles in the Bay of Biscay originating from the different rookeries is estimated using foraging ground centric analysis, computed with and without population size information. The proportion of individuals from each rookery that ends up stranded in the Bay of Biscay is estimated with rookery centric analysis. The latter excluded Mediterranean rookeries since foraging ground centric analysis showed little contribution from these populations. Mean and standard deviation (*sd*) values are shown. Abbreviations: Br, Brasil; ES-RJ: Espírito Santo-Rio de Janeiro. Further details of datasets used in the MSA are in supplementary tables S1 and S2 (Appendix4).

Rookery	**Relative population size**	**'many-to-many' foraging ground centric Mean (*sd*)**		**'many-to many' rookery centric Mean (*sd*)**
		No size	**Size**	**Size**
South Florida	0.6863	0.0623 (0.0517)	0.5107 (0.1041)	0.0410 (0.0242)
Northwest Florida	0.0061	0.0791 (0.0601)	0.0114 (0.0121)	0.0862 (0.0765)
Northeast Florida	0.0634	0.0842 (0.0595)	0.0775 (0.0596)	0.0645 (0.0507)
Dry Tortugas	0.0022	0.0587 (0.0474)	0.0040 (0.0044)	0.0881 (0.0812)
Mexico	0.0184	0.1575 (0.0562)	0.0718 (0.0351)	0.1901 (0.0775)
Bahía-Sergipe (Br)	0.0274	0.0117 (0.0114)	0.0115 (0.0113)	0.0225 (0.0266)
ES-RJ (Br)	0.0199	0.0118 (0.0118)	0.0104 (0.0104)	0.0282 (0.0334)
Cape Verde	0.1432	0.2242 (0.0687)	0.2601 (0.0805)	0.1038 (0.0697)
Greece	0.0212	0.0347 (0.0326)	0.0210 (0.0222)	-
Cyprus	0.0058	0.0433 (0.0401)	0.0095 (0.0111)	-
Lebanon	0.0004	0.0434 (0.0384)	0.0007 (0.0008)	-
Creta	0.0040	0.0418 (0.0366)	0.0066 (0.0078)	-
Israel	0.0003	0.0381 (0.0332)	0.0006 (0.0007)	-
Eastern Turkey	0.0010	0.0606 (0.0425)	0.0019 (0.0021)	-
Western Turkey	0.0013	0.0486 (0.0444)	0.0022 (0.0024)	-

Appendix 4

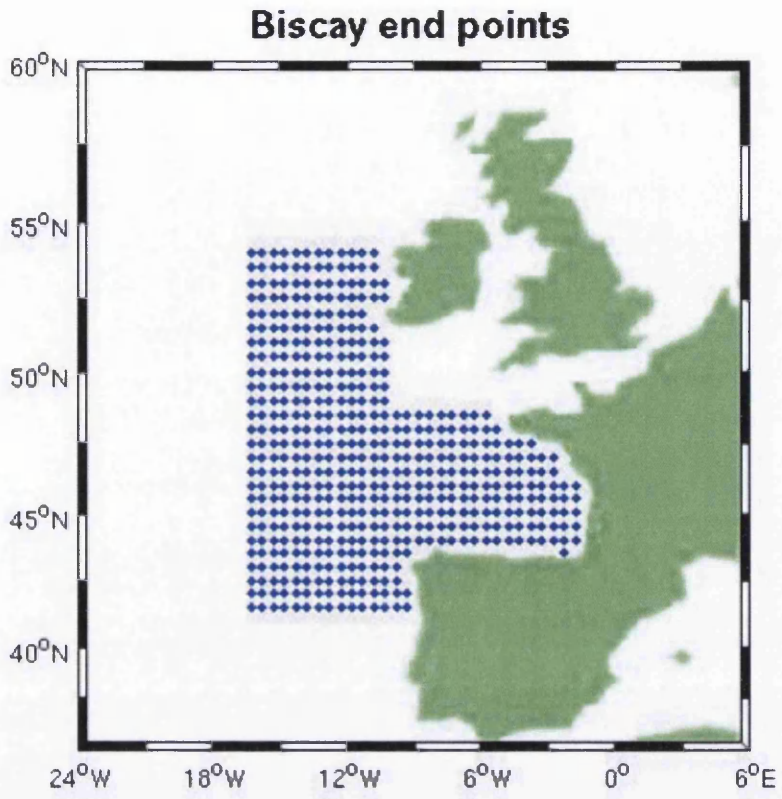

Fig. S1. The "end-points" in the Bay of Biscay region (rectangular mesh spanning 1.8–16.3° W and 41.5–54° N) from which particles are back-tracked for 3 years according to the hindcast surface currents of NEMO.

Table S1. Mitochondrial DNA control region haplotypes (~380 bp) for loggerhead nesting populations ("rookeries"). Haplotype frequencies and nesting population sizes used in the many-to-many mixed stock analysis are shown. Abbreviations: CV, Cape Verde; SFL, South Florida; NEFL-NC, Northeast Florida-North Carolina; NWFL, Northwest Florida; DT, Dry Tortugas; MEX, Mexico; BA-SE, Bahía-Sergipe (Brazil); ES-RJ, Espírito Santo-Río Janeiro (Brazil); GRE, Greece; CYP, Cyprus; LEB, Lebanon; CRE, Creta; ISR, Israel; ETU, Eastern Turkey; WTU, Western Turkey. Unpublished data for CV was added; other data were previously published (Encalada *et al.* 1998; Bowen *et al.* 2005; Carreras *et al.* 2007; Reis *et al.* 2010; Monzón-Argüello *et al.* 2010). Population sizes are based on published data (Ehrhart *et al.* 2003; Margaritoulis *et al.* 2003; Marcovaldi *et al.* 2007; Marco *et al.* 2008).

	Rookeries														
Haplotype	CV	SFL	NEFL-NC	NWFL	DT	MEX	BA-SE	ES-RJ	GRE	CYP	LEB	CRE	ISR	ETU	WTU
CC-A1	133	52	104	38	4										
CC-A2	2	45	1	7	50	11			54	35	9	19	17	19	15
CC-A3		4		2		2								13	1
CC-A4							63	113							
CC-A5		1													
CC-A6									5						
CC-A7		3		2											
CC-A8						1									
CC-A9					2	1									
CC-A10					2	5									
CC-A11	2	1													
CC-A12															
CC-A13															
CC-A14		2													
CC-A15															
CC-A16															
CC-A17	56														
CC-A20		1													
CC-A21															
CC-A24							13								
CC-A25								1							
CC-A26															
CC-A27															
CC-A28															
CC-A29													3		
CC-A30															
CC-A31															
CC-A32									1						
CC-A42															
CC-A46															
CC-A47	3														
Total	196	109	105	49	58	20	76	114	60	35	9	19	20	32	16
Pop size	**14,000**	**67,100**	**6,200**	**600**	**217**	**1,800**	**2,677**	**1,859**	**2,073**	**572**	**35**	**387**	**33**	**100**	**124**

Table S2. Mitochondrial DNA control region haplotypes (~380 bp) for loggerhead strandings and foraging grounds used in the many-to-many mixed stock analysis. FR, France; CAN, Canary Islands; MAD, Madeira; AND, Andalusia; AZO, Azores; LAM, Lampedusa; GIM, Gimnesia; PIT, Pitiüses; NES, Northeastern Spain; WIT, Western Italy; EIT, Eastern Italy. In addition to new data for stranded turtles, unpublished data was added for CAN; otherwise, all other data were previously published (Bolten *et al.* 1998; Carreras *et al.* 2006; Revelles *et al.* 2007; Monzón-Argüello *et al.* 2010).

	Mixed Stocks										
Haplotype	FR	CAN	MAD	AND	AZO	LAM	GIM	PIT	NES	WIT	EIT
CC-A1	37	90	24	45	36	17	16	9	14	4	2
CC-A2	31	52	19	46	31	39	11	17	81	40	48
CC-A3	6	8	2	2	5	3	3		8	3	5
CC-A4		1									
CC-A5								1	1		
CC-A6											
CC-A7		2				1			1		
CC-A8	1	1			1						
CC-A9	1			2		1		1			
CC-A10	4	7	3	1					1		
CC-A11			1	2							
CC-A12			1	1							
CC-A13	1				2	1		1			
CC-A14	1	1	1	2	2	1		2			
CC-A15					1						
CC-A16					1						
CC-A17	4	4	1	1							
CC-A20		2									
CC-A21				2							
CC-A24											
CC-A25											
CC-A26						2		1	2	1	1
CC-A27							1				
CC-A28									1		
CC-A29									2		
CC-A30									1		
CC-A31											1

CC-A32										1	1
CC-A42				1							
CC-A46		1									
CC-A47	1										
CC-A63	1										
CC-A64	1										
Total	**89**	**169**	**52**	**105**	**79**	**65**	**31**	**32**	**112**	**49**	**58**

Table S3. Haplotype composition of loggerhead strandings in the Atlantic coast of France. The table shows haplotype designation for the short traditionally used fragment (~380 bp) and the new longer fragment (~760 bp). Some haplotypes were considered to represent Cape Verdean (CV) or American (Amer) individuals – see text for more details. Haplotypes frequencies for the stranded group of turtles and the Cape Verde rookery (Monzón-Argüello *et al.* 2010) are shown. Data on survival (dead or alive), minimum straight carapace lengths (SCLmin) in centimetres and weights in grams are shown for each haplotype.

Short Haplotype	Long Haplotype	Group	France	Cape Verde	Alive/Dead	Mean SCLmin (range)	Mean Weight (range)
CC-A1	CC-A1.1	Amer	20 (0.23)		0.70/0.30	23.7 (12.5-61.5)	3,366 (375-30,000)
	CC-A1.3	CV	13 (0.15)	79 (0.62)	0.08/0.92	20.1 (16.7-24.2)	1,334 (590-2,160)
	CC-A1.4	-	4 (0.05)	6 (0.05)	1.00/0.00	20.1 (18.3-22.8)	1,383 (1,060-2,000)
CC-A2	CC-A2.1	-	30 (0.34)	2 (0.02)	0.60/0.40	22.4 (13.5-50.7)	2,300 (420-16,290)
	CC-A2.7	-	1 (0.01)		1.00/0.00	19.8	1,230
CC-A3	CC-A3.1	Amer	6 (0.07)		0.67/0.33	19.1 (15.0-24.0)	1,138 (550-1,800)
CC-A8	CC-A8.1	-	1 (0.01)		1.00/0.00	21.0	1,276
CC-A9	CC-A9.1	-	1 (0.01)		1.00/0.00	44.3	13,000
CC-A10	CC-A10.1	Amer	4 (0.05)		0.75/0.25	26.3 (18.9-32.6)	3,517 (1,200-6,350)
CC-A13	CC-A13.1	-	1 (0.01)		0.00/1.00	50.3	17,000
CC-A14	CC-A14.1	-	1 (0.01)		1.00/0.00	20.5	1,680
CC-A17	CC-A17.1	CV	4 (0.05)	30 (0.23)	0.25/0.75	21.2 (19.5-24.3)	1,808 (1,420-2,750)
CC-A47	CC-A47.1	-	1 (0.01)	1 (0.01)	1.00/0.00	19.0	950
CC-A63	CC-A63.1	-	1 (0.01)		0.00/1.00	22.8	2,020
CC-A64	CC-A64.1	-	1 (0.01)		1.00/0.00	21.8	1,500

Table S4. Haplotype *(h) and* nucleotide *(π)* diversity of the samples from juvenile loggerhead turtles stranded in the Bay of Biscay and from four proximal foraging groups: Azores and Madeira (Bolten *et al.* 1998), Andalusia (Revelles *et al.* 2007) and the Canary Islands (Monzón-Argüello *et al.* 2009) with 76 additional samples. Standard deviations (*sd*) are shown.

Location	***h (sd)***	***π (sd)***
Bay of Biscay (stranded group)	0.7043 (0.0324)	0.0342 (0.0172)
Azores (foraging group)	0.6407 (0.0331)	0.0340 (0.0172)
Madeira (foraging group)	0.6599 (0.0436)	0.0341 (0.0173)
Andalusia (foraging group)	0.6282 (0.0283)	0.0338 (0.0170)
Canary Islands (foraging group)	0.6171 (0.0289)	0.0330 (0.0166)

Table S5. Annual genetic composition of strandings in the Bay of Biscay (1995-2009). Relative haplotype frequencies for longer sequences are shown. Genetic differences across years were investigated using those with sample sizes > 7 individuals (n = 6).

Year	N	CC-A1.1	CC-A1.3	CC-A1.4	CC-A2.1	CC-A2.7	CC-A3.1	CC-A8.1	CC-A9.1	CC-A10.1	CC-A13.1	CC-A14.1	CC-A17.1	CC-A47.1	CC-A63.1	CC-A6
1995	1	1														
1997	5				0.80					0.20						
1998	11	0.09	0.09	0.18	0.36				0.09						0.09	0.09
1999	11	0.18	0.09	0.18	0.45	0.09										
2000	7	0.14			0.43		0.14			0.14		0.14				
2001	20	0.40			0.40		0.15	0.05								
2002	3		0.33				0.33				0.33					
2003	3		0.67							0.33						
2004	1				1											
2007	7	0.29	0.43							0.14			0.14			
2008	6	0.33	0.17		0.50											
2009	8	0.13	0.38		0.25								0.13	0.13		

Table S6. Pairwise comparison between different years using the exact test of population differentiation. Asterisks denote statistically significant values.

Year	1998	1999	2000	2001	2007	2009
1998	-					
1999	1.000	-				
2000	0.781	0.637	-			
2001	0.011 *	0.067	0.274	-		
2007	0.101	0.053	0.113	0.001 *	-	
2009	0.530	0.377	0.300	0.014 *	0.775	-

Table S7. Eleven Atlantic storms and hurricanes originated near the Cape Verde archipelago during the period studied. The name of the storm, year, class, maximum speed and dates are shown. Major Hurricane (MH), hurricane with wind speed 50 m s^{-1} or higher; Hurricane (H), wind speed 33-49 m s^{-1}; Tropical storm (TS), wind speed 17-32 m s^{-1}.

No	Name	Year	Class*	Max speed (m s^{-1})	Dates
1	Alberto	2000	MH	57	3 – 23 Aug
2	Isaac	2000	MH	62	21 Sep – 1 Oct
3	Fabian	2003	MH	64	27 Aug – 8 Sep
4	Danielle	2004	H	49	13 – 21 Aug
5	Karl	2004	MH	64	16 – 24 Sep
6	Maria	2005	MH	51	1 – 10 Sep
7	Debby	2006	TS	23	21 – 26 Aug
8	Florence	2006	H	41	3 – 12 Sep
9	Gordon	2006	MH	54	10 – 20 Sep
10	Helene	2006	MH	54	12 – 24 Sep
11	Bertha	2008	MH	57	3 – 20 Jul

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Chapter 5

Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals

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Functional Ecology (in press)

Disclaimer: RS and GCH conceived the study. RS compiled the data. RS and GCH wrote the manuscript.

Abstract

Some animals migrate huge distances in search of resources with locomotory mode (flying/swimming/walking) thought to drive the upper ceilings on migration distance. Yet in cross–taxa comparisons, upper ceilings on migration distance have been ignored for one important group, sea turtles. Using migration distances recorded for 407 adult and 4715 juvenile sea turtles across 5 species, we show that for adult cheloniid turtles the upper ceiling on species migration distances between breeding and foraging habitats (1050 to 2850 km across species) is similar to that predicted for equivalent sized marine mammals and fish. In contrast, by feeding in the open ocean adult leatherback turtles (*Dermochelys coriacea*) and juveniles of all turtle species can travel around 12,000 km from their natal regions, travelling across the widest ocean basins. For juvenile turtles, this puts their maximum migration distances well beyond those expected for equivalent sized marine mammals and fish, but not those found in some similar sized birds. Post hatchling turtles perform these long distance migrations to juvenile foraging sites only once in their lifetime, whilst adult turtles return to their breeding sites every few (generally ≥2) years. Our results highlight the important roles migration periodicity and foraging mode can play in driving the longest migrations and the implications for Marine Protected Area planning are considered in terms of sea turtle conservation.

Introduction

There has been prolonged debate about the evolution of migration across animals with diverse life histories (Alexander 1998; Hein *et al.* 2011) and migration forms an important component of the broader area of movement ecology (Nathan 2008). Migration is often described as the to-and-fro movement between regions where conditions (e.g. foraging/breeding conditions/temperature) are alternately favourable and unfavourable, so that it is better for animals to move between locations in some repeatable manner rather than remain continuously in one place (Dingle and Drake 2007; Holt and Fryxell 2011). Often this to-and-fro migration occurs over an annual cycle. Classic examples of these to-and-fro annual migrations include birds that may travel 100s or 1000s of km to take advantage of seasonally available resources and in some cases these movements span both the northern and southern hemisphere (Shaffer *et al.* 2006; Egevang *et al.* 2010). For example, satellite tracked Arctic terns *(Sterna paradisaea)* perform the longest documented animal migrations between their seasonal habitats in the Arctic and Antarctic > 17,000 km apart (Egevang *et al.* 2010). In the marine realm, there are also a number of notable long distant swimmers, including baleen whales which migrate to-and-fro between tropical calving grounds in winter and high latitude feeding areas in the summer (> 8,000 km apart; Rasmussen *et al.* 2007). In the terrestrial realm, migrants such as Arctic caribou *(Rangifer tarandus)* and wildebeest *(Connochaetes taurinus)* travel between sites several 100s km apart to avoid poor winter conditions and/or profit from good summer conditions (Fancy *et al.* 1989; Murray 1995).

For flying birds/insects, swimming mammals/fish and terrestrial mammals, meta-analyses show migration distances increase with species body mass, albeit with different relationships among flyers, swimmers and walkers: for their body size flyers travel furthest followed by swimmers and then walkers (Alexander 1998; Hein *et al.* 2011). Such relationships stimulate questions on the processes that drive maximum migration distances. Alexander (1998) considered the interplay between energy utilisation during migration, speed of migration and energy gain after completing migration to model potential migration distances across different taxa. For example, if animals travel quickly and the cost of migration is relatively small, then they may have sufficient time to build up reserves after

travelling to allow annual migration (Alexander 1998). The model of Hein *et al.* (2011) is centred around equations that relate the cost of locomotion to mode of locomotion (swimming, flying and walking), body size and movement speed. While this biomechanical model has great strength for predicting the observed general patterns of maximum migration distance, there remain a number of features related to specific aspects of the biology of individual taxa that may remain important, as evidenced by the considerable unexplained variation in migration distance not explained by the biomechanical model. For example, the model formulation of Hein *et al.* (2011) suggests that the number of re-fuelling stops during migration will influence the ceiling of migration distance. We use a paradigmatic group of long distance travellers, the sea turtles, which were not considered in the Hein *et al.* (2011) analysis, to explore two aspects of the biology of migrants that might be expected to be important determinants for maximum migration distance. First we consider the periodicity of migration. The general paradigm is that migrants complete to-and-fro migration each year. Hence there must be sufficient time to refuel within this annual cycle. However, sea turtles do not migrate every year, but instead take several years to re-fuel between migrations (Hughes 1995). Second we consider the importance of the extent of refuelling during migration trips by distinguishing species and life history stages of sea turtle that fast versus those that continually forage during long distance journeys.

Given the huge international efforts over the last decade devoted to satellite tracking sea turtles and also, to a lesser extent, to document the extent of juvenile movements using genetic mixed stock analysis (see for example Bowen and Karl 2007; Shillinger *et al.* 2008; Block *et al.* 2011), it is timely to review the distance that sea turtles migrate. We used satellite tracking and molecular mixed stock analysis of > 5000 individual sea turtles across 5 species to establish where their upper ceiling on migration distance lies compared to other walking, flying and swimming migrants. Hence we help complete the picture of how sea turtle migration distances compare to those of other vertebrates whilst taking into consideration the roles of breeding periodicity/migration frequency (annual versus non-annual), feeding mode during migration (feeding versus fasting) and locomotory mode (swimming, flying, walking) in driving migration distances.

Methods

Adult Migratory Distances

For adult hard shelled sea turtles (family Cheloniidae), we used papers in the peer review literature where maps clearly displayed the post nesting migratory routes of ≥ 3 individuals successfully satellite tracked to spatially discrete foraging sites (see Table S1a and supporting references in Appendix 5). Only turtles that showed a period of residence, typically weeks or months at their final destinations, were considered successfully tracked to foraging grounds. Whilst Cheloniidae species typically migrate to spatially discrete neritic foraging habitats, a couple of turtles were tracked to less discrete oceanic foraging habitats (e.g. loggerhead turtles from Cape Verde; Hawkes *et al.* 2006). Satellite transmissions confirmed that these individuals had reached their general foraging areas off the West coast of Africa as tags transmitted for prolonged periods (several months to > 1 year) in these offshore waters. Hence for these turtles, their final locations were used to represent the general vicinity of their foraging habitats. Other turtles believed to be foraging oceanically (e.g. green turtles tracked south from the Galapagos Islands; Seminoff *et al.* 2008) were not included in this analysis as their final foraging habitats could not be confirmed. Tags from these turtles either stopped transmitting whilst turtles were still travelling at speeds of 25 to 50 $km.d^{-1}$ or, at most, only two successive Argos fixes at the same oceanic locations where transmitted before tag transmissions ceased. Leatherback turtles (*Dermochelys coriacea*) are the only species of the family Dermochelyiidae. Unlike Cheloniidae species, adult leatherbacks do not migrate to discrete foraging sites where they remain for long periods, but instead they continue to travel throughout the interval between breeding seasons (e.g. Fossette *et al.* 2010). Hence for leatherbacks, we could not use migratory end points to identify foraging grounds. Consequently, in order to compare travel distances of adult turtles, we measured the great-circle distance (assuming travel around intervening land masses) between breeding grounds and the point at which turtles were furthest from their breeding grounds.

For > 99% of the tracked cheloniid turtles, great circle distance measurements revealed that final foraging destinations also coincided with the point of maximum displacement from nesting sites. So for two loggerhead turtle (*Caretta caretta*) populations where the furthest

locations of their tracks could not be determined (because individual tracks could not be identified in the spaghetti tracking plots of a large number of individuals) (Hawkes *et al.* 2006; Girard *et al.* 2009); we instead measured the distance to final foraging locations which were clearly identifiable. For leatherback turtles we only used populations where ≥ 3 individuals were tracked for a period of at least 4 months before satellite transmissions stopped. When the duration of the satellite tracking period was unknown, tracks which had clearly ended too prematurely to obtain accurate information on distance travelled (typically just a few km from the nesting site whilst individuals were still in transit to foraging sites or believed to be performing inter-nesting movements) were not used. In studies where individual leatherback tracks could not be identified in the spaghetti tracking plots of large numbers of tracked turtles, we instead measured distances to clearly defined high use foraging areas; areas of concentrated and prolonged foraging activity by one or multiple individuals (Shillinger *et al.* 2008; Benson *et al.* 2011). Where it was unclear, how many turtles had migrated to each high use foraging area, the number of tracked turtles were divided by the number of high use areas to best utilise these valuable extensive datasets to gain information on migration distances (Shillinger *et al.* 2008).

Juvenile Migratory distances

All sea turtles except the geographically restricted flatback turtle (*Natator depressus*) have a juvenile oceanic phase (Musick and Limpus 1997). Hatchlings enter the sea and disperse widely in oceanic currents for a period commonly known as the "lost years", until they are seen again upon arrival in coastal foraging habitats as young juveniles. Due to natal philopatry and the resultant genetic isolation among nesting populations, population specific mtDNA markers are routinely used to assign juvenile turtles captured at juvenile feeding grounds to their respective rookery of origin (Bowen and Karl 2007). Due to the evolving nature of this technique and the continual updating of mtDNA databases as genetic data from additional turtle rookeries are obtained for each juvenile foraging ground, we used only the most recent publication where mixed stock analyses had been conducted to determine the origin of and hence displacement distance of juvenile turtles. In the same way as adult turtles, displacement distances between foraging and nesting grounds were determined by great-circle distances assuming travel around land masses (see Table S1b

and supporting references in Appendix 5). These juvenile movements between nesting grounds and foraging sites may only occur once in each direction in an individual's life and hence are not "to-and-fro" migrations like those shown by adults. For simplicity, here we use the term "migration" to describe both the to-and-from movements of adults as well as these movements of juveniles.

Across taxa meta-analysis

The majority of satellite tracking studies contained data on the carapace measurements of individual turtles. Carapace measurements were converted to body mass (kg) based on species specific carapace length and mass equations (van Dam and Diez 1998; Jones, *et al.* 2008; Wabnitz and Pauly 2008). In a few instances where the sizes of satellite tracked individuals were not available we used either (a) the mean size of the satellite tracked turtles from that site or (b) the mean size of the nesting population at that site (see Table S1a in Appendix 5). Using R software (R Development Core Team 2009) Mann Whitney-Wilcoxon tests were used in pairwise comparisons to determine if migration distances differed significantly between cheloniid species, between adult leatherbacks and cheloniid species and between adult and juvenile turtles within species. For hard shelled turtles we used percentile regression to objectively fit a function to the upper ceiling of migration distance versus body size. We created a series of size bins (25-kg increments) and then determined the 97.5 percentile of the values for migration distance within each bin. The choice of a particular percentile threshold will have some influence on the function fitted for the upper ceiling of migration distance. We therefore conducted a sensitivity analysis to show that our conclusions were not changed by varying to percentile values between 90-99%. We chose the 97.5 percentile on the basis of statistical convention (i.e., the 95% confidence interval) (e.g. Bradshaw *et al.* 2007). For comparison of sea turtle migration distances compared to other groups, migration distances for other swimmers (marine mammals and fish), walkers (terrestrial mammals) and flyers (birds and insects) were taken from a recent meta-analysis (Hein *et al.* 2011) of species maximum recorded migration distances (typically displacement).

Results

Adult sea turtles

There were significant differences in the migration distances across adult sea turtle species (Fig. 1a and 1b; Table S1a in Appendix 5). For adults, mean migration distances (± SD) were 4,138 ±1,966 km for leatherbacks, 806 ± 602 km for green turtles (*Chelonia mydas*), 618 ± 445 km for loggerhead turtles, 327 ± 387 km for hawksbill turtles (*Eretmochelys imbricata*) and 482 ± 286 km for olive ridley turtles (*Lepidochelys olivacea*). Maximum migration distances were c.11,000 km (Benson *et al.* 2011) 2,850 km (Hays *et al.* 2002a), 2,150 km (Broderick *et al.* 2003), 1,630 km (vanDam *et al.* 2008) and 1,050 km respectively (Whiting *et al.* 2007). Within the cheloniid turtles, in order of descending mean/maximum migration distance, migration distances were significantly different between green turtles and loggerhead turtles (n=194, W_1=7120, P=0.04), loggerhead turtles and hawksbill turtles (n=110, W_1= 1050, P < 0.001) and hawksbill and olive ridley turtles (n=40, W_1=526, P=0.04; Fig 1b). Migration distances for leatherback turtles were significantly further than all the cheloniid turtles combined (n= 407, W_1 = 278891, P < 0.001; Fig. 1a). Species phylogeny thus appears to have had an important influence on adult migration distances. Across adult cheloniid turtles (i.e. excluding leatherback turtles) there was a weak linear relationship between migration distance and body mass: log10 distance (km) = 0.49 x log10 turtle body mass (kg) + 1.69 (n=234, R^2=0.03, F_{232}=7.26, P < 0.01). However the percentile regression indicated that the upper ceiling of migration distance did not increase significantly with body size (n=234, $F_{1,4}$=0.04, P=0.84). A weak linear relationship between migration distance and body mass was also evident for leatherback turtles (body mass: log10 distance (km) = 0.72 x log10 turtle body mass (kg) + 1.77 (n=173, R^2=0.03, F_{171}=6.24, P= 0.01).

Fig. 1. presents some examples of special cases for adult migration distance in cheloniid turtles, e.g. small turtles that migrated relatively long distances and large turtles that migrated relatively short distances. For example three small (c. 40 kg) loggerhead turtles from Cyprus migrated c.2000 km (Broderick *et al.* 2003), while large (c. 150 kg) green turtles nesting on the Cocos (Keeling) Islands were non-migratory (Whiting *et al.* 2008).

Also highlighted are the longest migrations shown by adult cheloniid turtles; green turtles from Ascension Island which migrated up to 2850 km (Hays *et al.* 2002a).

Juvenile sea turtles

Migration distances travelled by juvenile turtles were of the same order of magnitude as leatherback turtles (Fig. 1a, Table S1b in Appendix 5). The mean (±SD) distances travelled by juvenile green turtles, loggerhead turtles and hawksbill turtles were 4,557 (±2,525) km, 4,993 km (±3,627) km and 2,675 km (±3,212) km respectively. Within species, migration distances of juvenile turtles were significantly different to adult turtles (green turtles: n=1540, W_1 =39367, $P < 0.001$, hawksbill turtles: n=698, W_1 =5637, $P < 0.001$, loggerhead turtles: n=2686, W_1 =47511, $P < 0.001$). The maximum migration distances of > 13,000 km were obtained by juvenile loggerhead turtles that travelled from Australia to Peru (Boyle *et al.* 2009). Loggerhead turtles from the Mediterranean, Mexico and southern Florida travelled > 10,000 km (Casale *et al.* 2008; Rees *et al.* 2010). The maximum distances recorded for juvenile green turtles were > 9,000 km from West Africa to the southeast USA and juvenile greens from Ascension Island, eastern Brazil, Costa Rica, Mexico and Florida all travelled > 8,000 km (Monzón-Argüello *et al.* 2010). Juvenile hawksbill turtles from Mexico, Belize and Costa Rica travelled > 10,000 km to foraging grounds off West Africa (Monzón-Argüello *et al.* 2011). Species phylogeny also appears to influence juvenile migration distances as migration distances were significantly different between juvenile green and loggerhead turtles (n=4032, W_1=4854108, $P < 0.001$), juvenile loggerhead and hawksbill turtles (n=3274, W= 928319, $P < 0.001$) and juvenile green turtles and hawksbill turtles (n=2096, W_1=562336, $P < 0.001$).

Theoretical considerations

Is this observed maximum migration distance of c.2,850 km for adult cheloniid turtles close to the physiological maximum for a sea turtle that does not feed while away from the foraging grounds? Fig. 2 sets out some of the considerations which dictate when migration will be profitable. Quantifying the various rates of energy gain and expenditure inherent in these theoretical body condition trajectories is not straightforward in sea turtles. Almost nothing is known about the maximum fuel stores, the rate of energy loss when at the

breeding grounds and the rate of energy gain on the foraging grounds. However, we can crudely estimate, using best guesses to parameterise the energy balance calculations, if 2,850 km lies close to the physiological maximum that can be sustained by fuel stores. Green turtles nesting at Ascension Island are around 150 kg (Hays *et al.* 2002b) and a study of one species of turtle, the leatherback, revealed that turtles weigh approximately 25% more on their foraging grounds than on their nesting beaches (James *et al.* 2005). If we assume a maximum fat load to sustain migration of 25% of the total body weight, then for a 150 kg turtle we obtain a fat store of around 37.5 kg. The weight loss of female green turtles during nesting season at Ascension Island has been measured by repeat weighing individuals and averages 0.22 $kg \cdot d^{-1}$ (Hays *et al.* 2002b). These empirical data provide a good starting point for the energy/fat balance calculations. During the nesting season female turtles at Ascension Island rest for around 40% of their time during which their energy expenditure has been estimated from dive durations at 0.018 l O_2 $kg.h^{-1}$ (Hays *et al.* 2000), which is close to that predicted from allometric predictions based on minimal metabolic rates measured for turtles ashore on beaches (Prange *et al.* 1976). The energy content of an egg laid by a green turtle at Ascension Island is 279.5 kJ, the mean clutch size is around 110 eggs and individuals are thought to produce around 3 clutches per nesting season over about 40 days (Hays *et al.* 2000; Hays *et al.* 2002b). Direct observations and satellite tracking have shown that prior to the nesting season, green turtles are at Ascension Island for around 30 days to mate and that the Brazil-Ascension Island ocean crossings takes around 80 days (i.e. 40 days each way). Key uncertainties in fat utilization calculations are the metabolic rate of turtles when they are non-resting during the nesting seasons (i.e. 60% of their time); their metabolic rate during the 30 day mating season and their metabolic rate during the 80 day oceanic crossings. If we assume these metabolic rates are 2x, 2.5x and 3.5x the resting metabolic rate (RMR) respectively (these values are reasonable given the difference between RMR and field metabolic rates (Hulbert *et al.* 2004), then the measured weight loss of 0.22 $kg.d^{-1}$ translates to a weight loss of 8.6 kg during the 39 day nesting season, 4.8 kg during the 30 day mating season and 17.9 kg during the 80 day oceanic crossings, i.e. total weight loss of 31.3 kg which is close to the assumed maximum fat load of 37.5 kg, i.e. fuel stores seem to impose an upper ceiling on migration distance for adult cheloniid turtles. Clearly these calculations are very speculative

given the dearth of information on metabolic rates of migrating turtles and maximum fat stores.

Comparisons between sea turtles and other taxa

The maximum migration distances of adult turtles were comparable, and within the 95% predictive intervals, of equivalent sized swimming fish and marine mammals (Fig. 3). Adult leatherback turtles (size 330 kg) that travelled the furthest from their breeding areas (11,000 km; Benson *et al.* 2011), had migration distances comparable to the largest fish such as the whale shark (*Rhincodon typus*, mass 34,000 kg, maximum migration distance 13,000 km) (Eckert and Stewart 2001); the great white shark (*Carcharodon carcharias*, mass 550 kg, maximum migration distance 11,000 km) (Bonfil *et al.* 2005); the basking shark (*Cetorhinus maximus*, mass 3900 kg, maximum migration distance 9,500 km) (Gore *et al.* 2008) and the bluefin tuna (*Thunnus thunnus*, mass 240 kg, maximum migration distance 9,500 km). However, the maximum migration distance for juvenile sea turtles was significantly greater than that predicted for equivalent sized swimming fish and marine mammals: for a 19 kg loggerhead turtle the maximum migration distance was 13,040 km (Boyle *et al.* 2009) compared to a 95% predictive interval for an equivalent sized fish or marine mammal of 1,379 km (95% predictive limit 241-7,899 km; 95% confidence limit 1,002-1,897 km). Hence, whilst Hein *et al.* (2011) modelled the maximum migration distances travelled across a broad size range of walking, swimming and flying migrants, we extend this work by including data from sea turtles. Whilst adult turtle migrations were in the predicted range of equivalent sized marine mammals and fish, juvenile sea turtles migrated further than modelled relationship between body mass and travel distance of swimming migrants would predict.

Discussion

In the most general terms, our inclusion of sea turtles in the cross-taxa meta-analysis re-affirms the general impression that, for their body size, migration distance is greatest in flyers, intermediate in swimmers and shortest in walkers. However, within sea turtles there were clearly differences in migration distances across juveniles versus adult cheloniid turtles and also adult cheloniid turtles versus adult leatherback turtles and between

cheloniid turtles. If an upper ceiling on migration distance exists in sea turtles we expect that (a) this ceiling will be evident in the empirical data, e.g. some trans-ocean basin migration distances will not be evident by adults travelling between breeding and foraging sites, (b) animals that do not need to complete this regular to-and-fro migration (e.g. immature turtles that do not return to juvenile development habitats once reaching maturity) may forage much further from their natal sites than adults on their regular breeding migrations and (c) individuals that do not fast while travelling to and from their breeding grounds, may be freed of an upper ceiling migration distance constraint and instead conduct much larger migrations than adults that fast. Our findings are consistent with all these expectations. Our results suggest that despite only breeding every few years, for adult cheloniid sea turtles there is an upper ceiling on migration distance of around 2,850 km. In contrast juvenile sea turtles and leatherbacks can travel across the widest ocean basins. Essentially for the later two groups it is only the width of the World's oceans and their thermal tolerance (McMahon and Hays 2006; Witt *et al.* 2007) that constrains their maximum migration distance.

Given the caveats with the energy/fat balance calculations, one possibility that remains is that the observed ceiling of migration distance in cheloniid sea turtles does not represent a physiological performance maximum but rather that there is never any need for cheloniid sea turtles to migrate further because there are no suitable breeding grounds that are further than this distance from foraging grounds. If this hypothesis is correct then we might expect that juveniles would similarly always forage within 2,850 km of their breeding grounds, but this was clearly not the case. Juvenile turtles can forage > 13,000 km from their breeding grounds. For example, juvenile loggerhead turtles from natal areas in Australia undergo transoceanic migrations to foraging grounds as far away as Peru respectively (Boyle *et al.* 2009). It should be noted that the molecular analysis reveals the direct line one-way distance between nesting areas and foraging areas for juveniles. These distances, therefore, are not the total distance travelled by juveniles or necessarily the furthest distance that an individual travels from the nesting area. However, given the large number of these molecular studies it is likely that our analysis does capture the maximum straight-line distance between nesting and foraging areas for juveniles. Certainly ocean currents may be

instrumental in the transoceanic dispersal of hatchling turtles. As Hein *et al.* (2012) notes, species that interact strongly with currents may deviate from model predictions on migration distance. Hatchling turtles reside near the ocean surface and although they may show some limited directional swimming, their movement trajectory is dominated by surface currents (Scott *et al.* 2012a; Scott *et al.* 2012b). As they drift and grow, the swimming ability of juvenile turtles improves. So whilst some hatchlings are displaced by both ocean currents and storms to unsuitable distant sites and are doomed never to return to breed (Witt *et al.* 2007; Monzón-Argüello *et al* 2012), there is direct satellite tracking evidence that juvenile turtles tracked from distant foraging grounds do undertake long oceanic journeys from these distant sites back to their breeding grounds (Eckert *et al.* 2008; Peckham *et al.* 2011). For example, Eckert *et al.* (2008) tracked a 54 kg juvenile loggerhead turtle which travelled > 8000 km from the South coast of Spain to the coast of Nicaragua over a period of 363 days, while Peckham *et al.* (2011) tracked juvenile turtles travelling across the Pacific from foraging grounds off the coast of Baja California back towards their natal area of Japan (> 10,000 km apart). In a unique satellite tracking study, Nichols *et al.* (2000) tracked a 95kg captive reared adult-sized loggerhead turtle from its release (and initial capture site) off the coast of Baja California back to its natal Japanese nesting region. This individual was captured in its juvenile foraging grounds (weighing just 4 kg) and then kept in captivity for 10 years; hence this transoceanic migration is regarded as a delayed juvenile return migration as opposed to a typical to-and-fro adult breeding migration. Juveniles can presumably forage at such distant sites because they remain at these sites for many years and then only make one return journey to take up residence at new coastal sub-adult foraging grounds much closer to their breeding sites. So the situation for juvenile sea turtles differs from that of adults who conduct their to-and-fro breeding migrations every few years. Furthermore, juvenile sea turtles probably feed en route during these long journeys. For example juvenile loggerhead turtles have a broad range of prey, and likely feed on a range of pelagic invertebrates including crustaceans (e.g. pelagic crabs) and molluscs (Witherington 2002) as well as dead animals encountered.

It remains surprising why such long-distance migrations (> 10,000 km) are not evident in small fish (Schmidt 1922). One possibility is that the small fish are simply not amenable to

direct tracking (e.g. with satellite tags) and that indirect efforts such as mark-recapture/genetics analysis have currently underestimated the true extent of movements. Support for this possibility comes from recent tracking results from small fish. For example, inferred from the distribution of larvae the spawning grounds of European eels (*Anguilla anguilla*) are thought to be in the Sargasso Sea > 6,000 km away from the European Shelf (Schmidt 1922; Schmidt 1923). However, it is only recently that satellite tracking has started to directly document the long migrations of adult eels to these spawning grounds (Aarestrup *et al.* 2009). The developing eel larvae, like hatchling turtles, seem to depend largely on ocean currents for their movement as they travel back to Europe (e.g Bonhommeau *et al.* 2009).

As well as juveniles, adult leatherback turtles can also travel to sites very distant from their breeding grounds (Benson *et al.* 2011). Importantly leatherbacks are open ocean foragers, consuming a variety of gelatinous zooplankton. Hence when they are travelling in the open ocean away from their breeding sites, their body condition is not necessarily declining during open ocean crossings. In other words, leatherback turtles do not conform to the general paradigm for adult sea turtles of a discrete time during travel away from foraging grounds where they do not feed and so must lose body condition. Their poleward movements are constrained by sea surface temperature, with leatherbacks unable to tolerate water temperatures < 15°C for extended periods, and hence their broad-scale movements can span the width, but not the length, of ocean basins as they cannot penetrate into polar regions (McMahon and Hays 2006). This environmental niche provides a limit to the geographical areas occupied by leatherbacks, compared to groups such as large whales that are more eurythermal and can hence travel between tropical and polar regions (Rasmussen *et al.* 2007). Hence the areas occupied by migrating swimmers, walkers and flyers may be the result of both their capacity to travel different distances from their breeding sites along with their environmental tolerances.

The maximum distances travelled by adult leatherbacks away from breeding sites (11,000 km) are comparable to the distances travelled by some of the largest fish such as great white sharks and bluefin tuna. As with leatherback turtles, these fish are presumably

foraging en route and hence the upper ceiling for their long distance movements are not simply driven by body reserves. For example, tracking data for great white sharks travelling from South Africa to Australia shows regular deep diving to 900m alternating with periods at the surface consistent with foraging for pelagic fish and cephalopods (Bonfil *et al.* 2005). Similarly there is evidence that some fish that travel long distances also do not breed every year. For example, bluefin tuna tracked using light based geolocator tags may show several years of residence in the western Atlantic and then NE Atlantic before returning to their breeding grounds in the Mediterranean (Block *et al.* 2005).

In short, our results suggest that freed of the constraint of fasting during long-distance movements, leatherback turtles and juvenile turtles may travel very large distances (> 10,000 km) across oceans from their natal regions akin to some large fish, but that in contrast, for adult cheloniid turtles the tendency to fast during migration between breeding and foraging sites seems to constrain their migration distance to below 3,000 km. Whilst these non-annual breeding migrations of adult cheloniid species should increase their capacity to migrate longer distances (as they have longer to replenish energy reserves) this 3,000 km migratory ceiling suggests that foraging mode during migration ultimately caps the attainable travel distances on these regular (albeit, non annual) to-and-fro migrations. Finally our results may have implications for marine conservation planning. In recent years some huge ocean areas that host populations of endangered sea turtles have been designated as Marine Protected Areas (MPAs) including Papahānaumokuākea Marine National Monument in the Pacific and the British Indian Ocean Territory (BIOT) MPA which encompass 360,000 km^2 and 639,661 km^2 respectively (Gerber *et al* 2011; Sheppard *et al.* 2012). However even these largest MPAs are unlikely to encompass the extent of movements undertaken by juvenile sea turtles originating from nesting beaches within those MPAs. Hence our results suggest that as well as MPA designation there is also on-going need for basin-wide conservation measures (e.g. methods to reduce sea turtle by-catch) to protect sea turtles.

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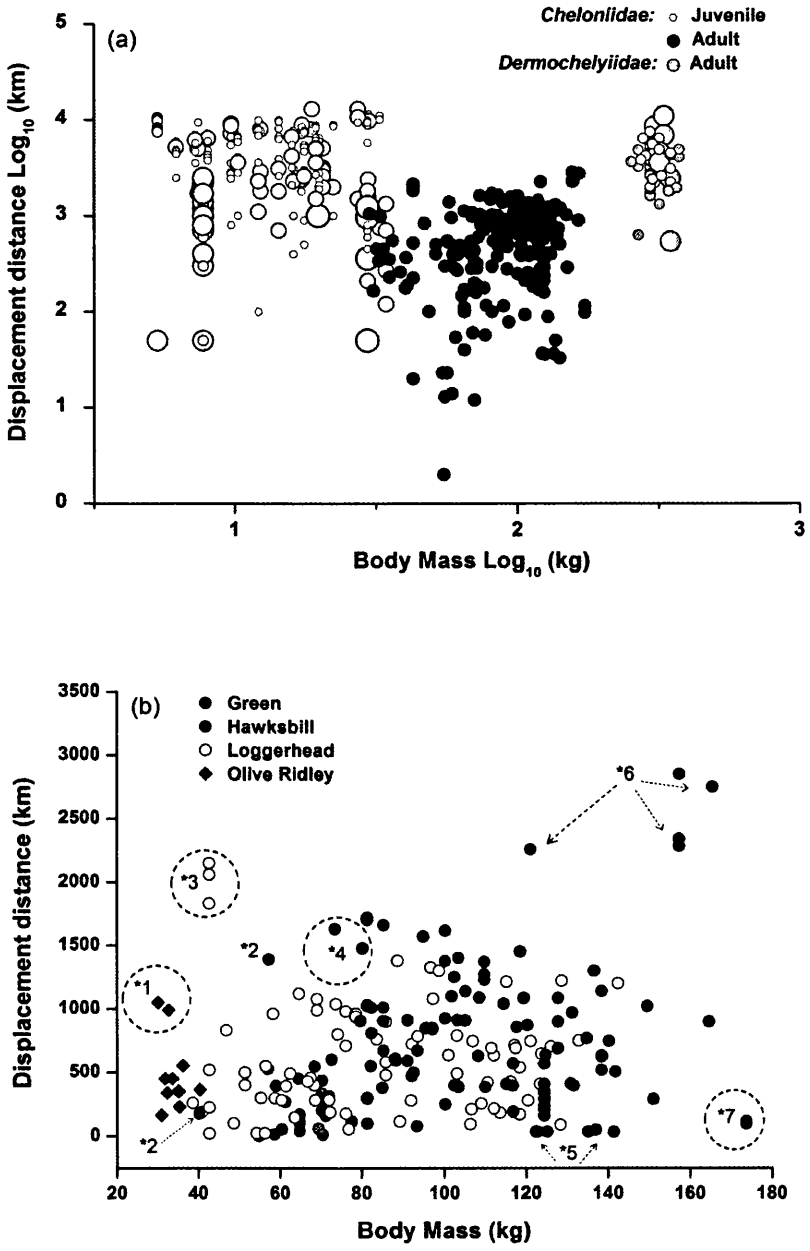

Fig.1. The distances between breeding sites and foraging sites for adult and juvenile sea turtles. Adult data comes from satellite tracked individuals (see Table S1a in Appendix 5). Juvenile data comes from genetic mixed stock analysis linking haplotypes on foraging grounds to potential source breeding grounds (see Table S1b in Appendix 5). (a) Data for all turtles. Data points for hard shelled adult turtles are based on each satellite tracked individual turtle. For leatherback turtles, small points represent data from a single individual and medium sized points represent the mean

distances travelled by 5-16 individuals. For juvenile turtles, the small points represent the distances travelled by < 10 individuals, medium sized points represent the distances travelled by ≥ 10 to < 100 individuals and large points represent the distances travelled by ≥ 100 to < 1000 individuals. (b) Only data for adult hard-shelled turtles. Asterisks denote points of interest; *1. Two Olive Ridley turtles that migrated c.1000 km from North Australia (Whiting *et al.* 2007; McMahon *et al.* 2007), *2. The smallest satellite tracked green turtle which did not migrate far from the Galapagos Islands and a small Galapagos green turtle that migrated > 1000 km after nesting are both highlighted (Seminoff *et al.* 2008), *3. Three small loggerhead turtles from Cyprus that migrated c.2000 km (Broderick *et al.* 2003), *4. The only two Hawksbill turtles to migrate > 1000 km (both from Puerto Rica; Van Dam *et al.* 2008), *5 Non migratory green turtles from the Cocos (Keeling) islands (Whiting *et al.* 2008), *6. Green turtles from Ascension island which performed the longest migrations of up to 2850 km (Hays *et al.* 2002a) and *7 Two large green turtles tracked (from Thailand) which did not migrate far (Yasuda *et al.* 2006).

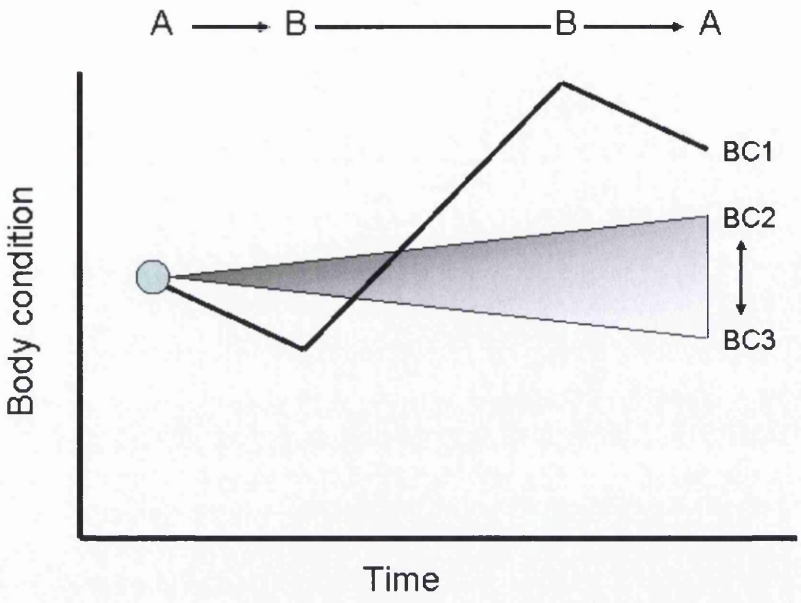

Fig. 2. Theoretical considerations for when migration will be feasible between two sites A and B for a sea turtle that loses body condition when migrating. The same considerations apply to other migrants that travel between breeding and foraging grounds. Green circle shows body condition of an individual at the end of the breeding season. Shaded area shows a range of body condition trajectories if the animal remains at the breeding ground A. The solid line shows the body condition of an animal that migrates to site B. In this situation body condition initially declines as the animal travels to site B, but then improved conditions at site B lead to a greater rate of increase in body condition compared to if the animal remained at site A. Consequently even after the animal migrates back to site A, its body condition (BC1) is better than if it had not migrated (range BC2 to BC3).

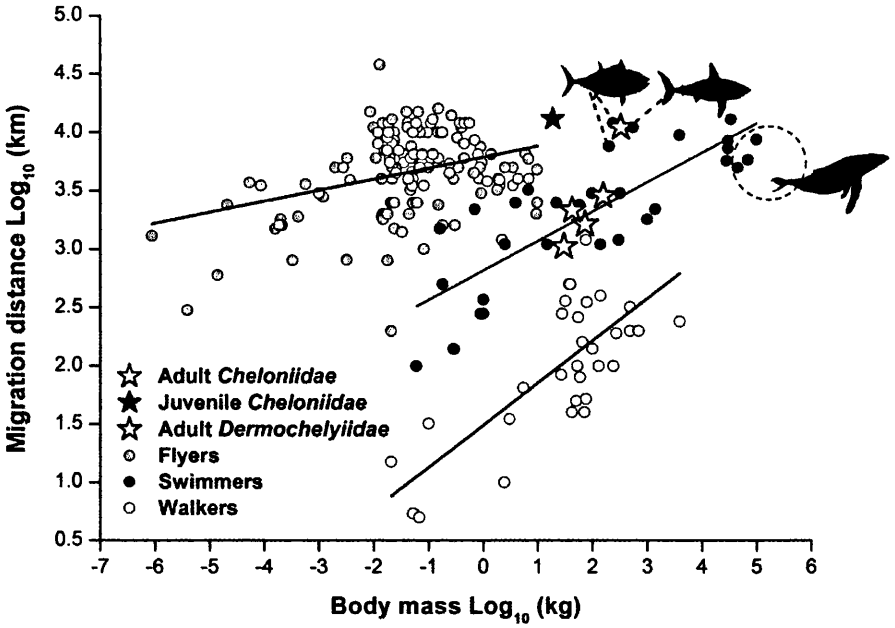

Fig. 3. Maximum migration distances for sea turtles (our study) compared to other swimming, walking and flying migrants (Hein *et al.* 2011). The upper migratory ceilings for adult turtles (10,000 km, 2850 km, 2150 km, 1630 km and 1050 km for leatherback turtles, green turtles, loggerhead turtles, hawksbill turtles and olive ridley turtles (Benson *et al.* 2011; Hays *et al.* 2002a; Broderick *et al.* 2003; Van Dam *et al.* 2008; Whiting *et al.* 2007) respectively) lie within the 95% predictive limits for other swimmers. However, the migration ceiling for juvenile sea turtles (13,040 km traveled by a 19 kg loggerhead turtle; Boyle *et al.* 2009) lies beyond the 95% predictive limit for other swimmers.

Appendix 5

Table S1a. Adult satellite tracking data. There was great variation in migration distances. For example, all hawksbills from the Seychelles remained within territorial waters of the Seychelles < 200 km from breeding grounds, some Caribbean hawksbills from Puerto Rico and Mediterranean loggerheads nesting in Cyprus and Zakynthos did not migrate more than 25 km from nesting grounds, whereas some of their conspecifics migrated > 1000 km. For green turtles breeding on the Cocos (Keeling) Islands in the Indian Ocean, no individuals migrated away from this small archipelago at the end of the breeding season, whereas green turtles breeding at Ascension Island in the Atlantic Ocean all migrated > 2000 km to foraging grounds off the coast of Brazil. Some olive ridley turtles from Australia migrated < 400 km, whilst others migrated c.1000 km. Leatherback turtles performed the longest migrations, with migrations of > 10,000 km observed in the North Pacific from individuals tracked from Indonesia to California.

(a) Adult Turtles	N	Max distance (km)	Mean distance (km)	Mean mass (kg)	Reference
Green					
(Chelonia mydas)					
Atlantic					
Ascension island	6	2850	2470	153	[1,2]
Cayman Island	7	900	729	132	[3]
Costa Rica	10	1089	512	117	[4]
Guinea Bissau	4	1140	1115	124	[5]
Indian					
China	6	1450	687	100	[6.7]
Cocos (Keeling) Island	6	50	38	131	[8]
Japan	3	1250	1000	150	[9]
Malaysia	4	1616	1131	97[6]	[10,11]
North Australia	20	570	332	126	[12]
Taiwan	8	1400	702	115	[13]
Thailand	7	672	488	121	[14]
Mediterranean					

Cyprus	10	1720	1053	81[15]	[16,17]
Pacific					
American Samoa	8	1370	1159	121[18]	[19,20]
French Frigate Shoals	8	1010	922	90	[19,21,22]
Galapagos Islands	4	1660	1199	69	[23]
Hawksbill					
(Eretmochelys imbricata)					
Atlantic					
Barbados	4	435	313	50	[24]
Costa Rica	2	451	361	45	[25]
Mexico	3	595	413	53	[26]
Puerto Rico	15	1630	379	50	[27]
Indian					
Seychelles	5	170	116	61[28]	[29]
Loggerhead					
(Caretta caretta)					
Atlantic					
Cape Verde Island	10	1378	674	68	[30]
Cayman Island	3	790	607	108	[3]
East Florida	28	1221	480	101	[31]
North Carolina	11	800	550	108	[32]
South Africa	3	900	653	86[33]	[34]
Mediterranean					
Cyprus	10	2150	830	42	[16,35]
Zakynthos	16	1120	733	69	[36–38]
Olive ridley					
(Lepidochelys olivacea)					
Indian					
Tiwi Islands	7	1050	438	35	[39]
Wessel Islands	4	990	558	33	[40]
Leatherback					
(Dermochelys coriacea)					
Atlantic					
French Guinea/Suriname	13	6400	4282	312	[41,42]
Gabon	20	7500	3629	300	[41,43]
Grenada	9	6230	4359	296	[44]
Panama	3	5600	3533	309	[41]

South Africa	6	3100	2542	349	[45]
Trinidad and Tobago	3	6400	4867	318	[46]
Pacific					
Costa Rica	46	4850	3783	269	[47]
Indonesia	73	11,000	5657	338	[48]

Table S1b. Juvenile mixed stock analysis data. Juvenile hard shelled turtles traveled distances much greater than adult hard shelled turtles and of the same order of magnitude as leatherback turtles. Whilst 6 % of juvenile hard shelled turtles only traveled c.50km (e.g. Hawksbill turtles in the Caribbean and gulf of Guinea and loggerhead turtles from south east Florida), 30% of turtles traveled between 100 and 1000 km and the majority (64%) traveled between 1000 km and 14,000 km. The maximum migration distances of > 13,000 km were obtained by loggerhead turtles that travelled from Australia to Peru/Brazil. Green turtles travelled > 9000 km from West Africa to the southeast USA. Hawksbill turtles from Mexico, Belize and Costa Rica travelled > 10,000 km to foraging grounds off West Africa.

(b) Juvenile Turtles	**N**	**Max distance (km)**	**Mean distance (km)**	**Mean mass (kg)**	**Reference**
Green					
(Chelonia mydas)					
Atlantic					
Ascension	134	8100	5011	16	[49,50]
Brazil	80	8100	4111	17	[49,50]
Costa Rica	195	8300	4525	16	[49]
Gulf of Guinea	83	9900	5900	16	[49,50]
Mexico	58	8800	4367	17	[49,51]
SE US	28	8500	3386	16	[49]
Surinam	61	5100	3125	16	[49]
Pacific					
French Frigate Shoals	787	1000	1000	20	[51]
Hawksbill turtle					
(Eretmochelys imbricata)					

Atlantic					
Antigua	28	7760	2293	7	[52–55]
Barbados	183	7480	2547	7	[52–55]
Belize	21	10,500	3280	7	[52–55]
Costa Rica	14	10,090	3673	7	[52–55]
Cuba	147	9770	2337	7	[52–55]
Gulf of Guinea	67	50	50	5	[54]
Mexico	86	10,600	3133	7	[52–55]
Puerto Rico	86	8270	1953	7	[52–55]
US Virgin Islands	32	8120	2128	7	[52–55]
Venezuela	2	8220	8220	5	[54]
Loggerhead turtle					
(Caretta caretta)					
Atlantic					
Brazil	69	5790	4432	15	[56–58]
Cape Verde	23	2860	2223	8	[58]
Mexico	75	11,100	5826	20	[56,57,59–62]
SE US	2028	10,100	4956	20	[55,58–62]
Indian					
Australia	60	13,040	12,480	25	[56,63,64]
Mediterranean					
Crete	1	4050	3395	9	[58]
Cyprus	62	4800	2770	18	[58,61]
Greece	159	10,740	4061	17	[56–59,61]
Turkey	54	11,540	5316	21	[56,57,59,61]
Pacific					
Japan	92	9800	9800	30	[64]

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Chapter 6

Evidence-based marine protected area planning for a highly mobile endangered marine vertebrate

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Disclaimer: RS conducted all the GIS/spatial analysis. GS and GCH conceived/lead the study. GS, SF and MKSL conducted the fieldwork. GS and KAK compiled the data. GS wrote the paper with contributions from all authors.

Abstract

Marine Protected Areas (MPAs) now form an important part of marine conservation and fisheries management; hence, there is broad interest in developing procedures that optimize their design. We used data collected over a 10-year period (2003–2012) from direct surveys and > 100 adult male and female loggerhead turtles (*Caretta caretta*) tracked with devices, including GPS loggers and Fastloc GPS-Argos, to consider the optimum design for a MPA at a globally important breeding area, where there is already an existing national marine park aiming to protect the endangered population (Zakynthos, Greece). Turtles primarily used areas very close to shore (approx.7 km length by 1 km width, within the < 10 m isobath) for breeding and foraging activity at different times of the year. We calculated that this small nearshore coastal zone encompassed 72% of all turtle GPS locations recorded in the MPA, and is therefore important for conservation management. We developed an index to evaluate the suitability of the existing and proposed conservation zones based on (1) the home range area use by turtles in these zones versus (2) the size of the zones, so that the benefit to turtles could be maximized while minimizing the negative impacts to other stakeholders (e.g. boat operators). With this evidence-based approach, we propose a modification to the existing MPA that might both enhance local economic tourism activities and better safeguard this key sea turtle breeding population. The approaches used here will have general application for the design of MPAs used by mobile species that can be tracked.

Introduction

Over the last two decades there has been a rapid increase in developing procedures for optimizing the design of Marine Protected Areas (MPAs) worldwide (McCay and Jones 2011). In theory, MPAs should conserve marine biodiversity, maintain productivity, and contribute to economic and social welfare (Christensen 1996; Pressey *et al.* 2007). it is unrealistic to assume that complete knowledge about the biodiversity, current and potential threats, or the effectiveness of management strategies may be obtained within a planning area. Hence, significant gaps often remain in the design and functioning of MPAs (Botsford *et al.* 2003; Sale *et al.* 2005; Agardy *et al.* 2011). In general, ecosystem approaches are advocated over a single-species approach when designing and evaluating the effectiveness of MPAs (Agardy 1994; Freidlander *et al.* 2007). Yet, more is often known about specific species targeted for protection than other components of the ecosystem (Hooker *et al.* 1999; Taylor *et al.* 2007). Within MPAs, the spatial placement of zones (or marine spatial planning) allows or restricts different anthropogenic activities, serving as the primary management mechanisms for protecting biodiversity and/or target species. In addition, many species of concern are migratory; hence, some areas (e.g. foraging or breeding areas) may only be vulnerable at certain times of the year, requiring seasonal rather than year-round protection. Therefore, zones require systematic planning for optimal delineation (Fernandes *et al.* 2005; Leslie *et al.* 2003; Witt et al., 2008).

Information about the spatial and temporal movement patterns of individuals is increasingly used to identify area use by terrestrial, avian and marine animals, and therefore sites worth protecting (e.g. dolphins; Hooker *et al.* 1999, caribou; Johnson *et al.* 2004, geese; Jensen *et al.* 2008, turtles; Scott *et al.* 2012). In marine environments, trends in animal spatial distributions are often determined by both fixed features (such as topography) and variable oceanographic features (such as temperature and salinity) (Hooker *et al.* 1999; Ardron *et al.* 2008). In general, MPAs based on static (e.g. bathymetry) or persistent (e.g. tides) environmental features are easier to implement (Hooker *et al.* 1999; Hyrenbach *et al.* 2000) than transient oceanographic or environmental features (Hooker *et al.* 2002; 2011; Ardron *et al.* 2008). Furthermore, these different approaches require different levels of environmental and wildlife data input. In theory, by obtaining baseline information about the requirements of target species and associated indicators, it is possible to develop programs that reduce threats

to species, while enhancing economically important anthropogenic activities. However, the updating of existing MPAs presents logistical and governance issues, particularly when delineated using precautionary rather than science-based information (Thompson *et al.* 2000). Hence, zones might not necessarily be representative of the endangered population they are designed to protect. To redress this discrepancy, long-term field monitoring techniques are crucial for conducting population/species level assessments (e.g. Scott *et al.* 2012). Such effort requires stable funding, a baseline understanding of key species, and the correct interpretation of assimilated data to objectively drive policy change (Pullin *et al.* 2004; Sutherland *et al.* 2004). Here we consider this important role of the extent of animal movements (e.g. Hays and Scott, 2013; Pala, 2013) for the optimal planning of MPAs.

While sea turtles often migrate 1000s of kilometers between breeding and foraging grounds, adult males and females tend to aggregate for several months at discrete breeding areas to mate and nest (Henwood 1987), presenting ideal sites for implementing protected area management. However, information remains limited about temporal shifts in spatial area use across this period by both sexes, with most studies focusing on inter-nesting female activity, as they are easier to detain for instrumentation when emerging on beaches to nest. Within the Mediterranean, the Greek island of Zakynthos is a well-established MPA and national park that, within its boundaries, primarily safeguards the breeding habitats of the largest population of endangered loggerhead sea turtles in the region. However, legislation for marine zoning was first implemented in 1991 with the establishment of zones A and B and completed in 1994 with the establishment of zone C (9 and 6 years before the establishment of the national park), and was based on nesting beach use by female sea turtles, rather than the actual marine habitat requirements of both sexes (for more details see Schofield *et al.* 2007). The marine protected area is primarily subject to two major uses (1) year-round commercial fishing, and (2) boat-based wildlife watching of sea turtles from May to September, while water-sport activity is prevalent along the island's eastern coastline.

Several tracking studies (Schofield *et al.* 2007; 2009ab; 2010ab; Zbinden *et al.* 2007; 2011; Hays *et al.* 2010; Fossette *et al.* 2012) have contributed preliminary insights about the marine area use, physiological requirements and environmental drivers, as well as providing tentative suggestions for protection of this population. However, the

effectiveness of existing legislation at safeguarding this breeding population has not been addressed, because these studies were (1) biased towards one sex, (2) of limited duration, and (3) based on small sample sizes (< 20 individuals) and small volumes of data that might not be representative at the population level (Borger *et al.* 2006; Murray 2006; Lindberg and Walker 2007; Schofield *et al.* in press). For instance, our research group has previously suggested that males and females occupy similar areas during the breeding period (Schofield *et al.* 2010a); however, this study was limited to just May and June, with a sample size of just 13 females and seven males. Here, we used data assimilated from 109 tracked (including GPS loggers and Fastloc GPS-Argos) males and female turtles, in addition to direct in-water surveys, over a 10 year period, as a case study to determine the utility of evidence-based information to pragmatically improve existing protection measures and drive policy change. We use the data to (1) map year-round habitat use by this adult breeding population using GIS and R software, (2) evaluate the effectiveness of existing zoning with respect to temporal and spatial use by the turtles, and (3) model the effectiveness of theoretical park boundaries using kernel analyses to identify core areas used by turtles and thus the optimum zoning that maximizes protection, while minimizing space restrictions for anthropogenic use (i.e. commercial fishing and turtle-watching ecotourism activities). Based on our findings, we consider the importance of both maximizing the protection of endangered species and the logistics of practical implementation of legislation at a governmental and local level.

Methods

Instrumentation

Between 2007 and 2012, a total of 77 loggerhead turtles (n = 45 males, of which six were tracked for more than one breeding season; n = 32 females of which one was tracked for more than one breeding season) from the Greek island of Zakynthos in the central Mediterranean basin (Fig. 1; 37° 43′ N, 20° 52′ E), were instrumented with satellite transmitters or TrackTag GPS dataloggers. During May of 2007 to 2012, the Swansea University team attached 53 transmitters and loggers (40 and 13, respectively), with a further 25 transmitters being attached from 2008 to 2010 under the NMPZ management authority, when males and females aggregate to mate before the start of the nesting season. This paper presents previously unpublished tracking information for seven male turtles.

In addition, the Swansea University team attached 12 TDRs (time-depth recorders) to females from 2006 to 2010 (Schofield *et al.* 2007; 2009ab; Fossette *et al.* 2012), for which information on the first nesting date was used in the current study. Furthermore, nesting and departure dates of the 18 turtles tracked by Zbinden *et al.* (2007; 2011) from 2004 to 2007 were incorporated into the analysis. We also included information from one turtle tracked by Casale *et al.* (2012) using an Argos-1010 transmitter; the transmitter was attached in the vicinity of Lampedusa Island, Italy, and the turtle resided in the breeding area of Zakynthos from 25 December 2006 to 25 February 2007.

All turtles were captured at sea, within 1 km of shore, in the vicinity of the nesting beaches (for methodology, see Schofield *et al.* 2007). When possible, transmitters were retrieved one year after attachment, during in-water surveys or on the nesting beaches. Units provided either GPS quality locations and/or Argos quality locations relayed either via the Argos satellite system or the mobile phone network. Table S1 (Appendix 6) lists the tracking devices used, with information on device programming, performance metrics and weights being available in our previous publications (Schofield *et al.* 2007; 2009a; 2010a; Fossette *et al.* 2012).

Information about attachment date, first nesting (females), departure date (all turtles) and return date in a subsequent season (males and females) are detailed in Table S1 (Appendix 6), along with unit type and turtle carapace curved length (CCL) measurement. All turtles were identified using a previously validated photo-identification system (Schofield *et al.* 2008). In addition, external flipper tags were used to identify females, with all captured turtles from 2008 onwards also receiving PIT identifiers. From May 2009 onwards, following confirmation that males (Hays *et al.* 2010), like females (see Broderick *et al.* 2007), return to their primary foraging sites, transmitters were primarily attached to previously untracked individuals, using the combined methods of identification. In the event of capturing previously tracked turtles, the individual was measured, photographed, identified, marked with paint (to avoid repeat captures in the same two week period), and returned to the sea. Transmitters were not attached to turtles with signs of recent injury, large numbers of leeches, emaciation, or flipper trauma/loss.

Breeding seasonality

The dates of arrival at and departure from the breeding area by migratory males were used to infer the start and end of breeding behavior of the males. For males that were resident to the breeding area, a complete shift (location and/or bathymetry) in home-range area was used to infer this transition at the start and end of breeding. The mating dates were assimilated from (1) direct boat-based transect surveys from April to July in 2003 (see Schofield *et al.* 2009a), (2) snorkel-surveys from April to July 2004–2005 (see Schofield *et al.* 2009a for details), (3) boat-based surveys for transmitter attachment in May 2006–2012, (4) opportunistic boat-based and/or snorkel surveys from April to July in 2006–2011, and (5) opportunistic land-based observations during daylight hours on a daily basis from February to July 2003–2011 (see Hays *et al.* 2010). Turtles mate both at the surface and in the water column/on the seabed; therefore, the assimilated datasets are biased to the former (i.e. surface mating activity), and should be treated as a cautious underestimate.

All units (transmitters and loggers) from Swansea University were attached in early May prior to the first recorded nesting event in all years, while NMPZ units were attached from May to July. Therefore, the first (and subsequent) nesting event was inferred by the units recording females on the beach for a minimum of 40 min (for GPS units this was identified by a drop in ambient temperature concurrent with depth measures at sea surface level; Schofield *et al.* 2007; Fossette *et al.* 2012), in parallel to confirmed visual observations of turtles on the beach by personnel from Swansea University, NMPZ, or the non-governmental organization (NGO) Archelon personnel conducting night surveys of nesting turtles. Departure from the breeding area was estimated as the first date that GPS locations were outside of the breeding area, and resulted in continued migration to a foraging area (i.e. excluding inter-nesting forays). The information on turtles tracked by Zbinden *et al.* (2007; 2011) was obtained from the publications.

Nesting information was collected from 2007–2009 under the field supervision of the lead author (GS) within the framework of a Sea Turtles Research Program directed by the National Marine Park of Zakynthos. During this period, both laying and hatching activity were monitored through daily dawn beach patrols. The position of all emergences and resultant nests were recorded in relation to marker posts placed at 20–

50 m intervals at the back of the beach and the geographic position of each nest was recorded using a handheld Garmin GPS unit (eTrex Legend, accuracy < 3 m, 95% typical; Garmin Ltd.), which together allowed 100% correlation with laid and hatched nests.

All dates were converted to day of the year for consolidation of datasets across all years. All datasets (male arrival, male departure, mating, onset of nesting by females, female departure, and nesting) were converted to percentages for compilation on a single graph. The last male arrival, first male departure, last female first nest, and first female departure were ranked as 100%. The peak mating and nesting numbers were ranked as 100%, with ascending and descending percentages on either side of the peaks.

Home range analysis

GPS locations were filtered by (1) subjectively removing visually erroneous locations (e.g., on land), and (2) using a maximum rate of travel of 5 km h^{-1} between successive locations (Luschi *et al.* 1998), which was selected based on calculations from three or more consecutive fixes occurring at 10–20 min intervals. Because of differences in data volume per turtle (particularly between archived and transmitted GPS locations), the datasets were further filtered to allow comparative analysis among all turtle datasets. This adjustment is important to prevent data point bias to a specific site as a result of certain individuals. Hence, the median GPS location per day for transmitted and retrieved archival data was selected for each turtle (Swihart and Slade 1985; Makowski *et al.* 2006; Tremblay *et al.* 2006; Schofield *et al.* 2010a) to conduct objective analyses of spatial and temporal area use. Sites were determined by turtles staying in residence for at least 7 days at a general area (see Zbinden *et al.* 2011). Migratory tracks along the coast were excluded, along with the data point on the day of departure from the island, as this was viewed as migrating data rather than local area use data.

To evaluate home range use by turtles, GPS locations were plotted using the World Geodetic System (WGS84; 1984) in ESRI ArcGIS® (version 10.0) software. and the cylindrical equal area projection was used for all spatial analysis. This projection provided a good representation of turtle home range areas, enabling accurate measurements. Habitat use of male and female turtles (separately and combined) was assessed using Gaussian kernel analysis to identify core use areas

(defined as the 50% kernel utilization distribution; Worton 1989; Borger *et al.* 2006; 2008) and total home range area (using both the 90% and 95% kernel utilization distributions; Borger *et al.* 2006). Kernel analysis were conducted using the kernel density tool in the Geospatial modeling environment (Beyer 2012) and bandwidth estimation algorithms in the 'ks' R software package (R Development Core Team 2011). Since kernel estimators are highly sensitive to bandwidth algorithms and the most appropriate bandwidth is dependent on the pattern of animal space use and sample size of locations (e.g. Gitzen *et al.* 2006), we tested the performance of the different bandwidths in the "ks" package with regards to capturing the area of sea used by turtles. The PLUGIN bandwidth was selected for all spatial analysis as it consistently performed better than the other bandwidths which tended to produce over smoothed kernels (that captured areas not used by turtles) or kernels that were too fragmented/focused on tight clusters of locations (hence missing key areas used by turtles).

Optimization of MPA design

To propose methods to improve existing MPA structure, we used the core area (based on the 50% core area) for all male turtles, all female turtles and both sexes combined to design a new zone that maximally protected the core marine area used by this population. We then developed an "effectiveness" index of the MPA for each month of the year, in which we calculated the actual area use by turtles versus the area of protective zoning (current and proposed), to determine maximal area use by turtles while minimally restricting anthropogenic use. This index of "effectiveness" was calculated to evaluate the suitability of the existing and proposed MPA zones based on (1) the 90% kernel area use (i.e. total home range area; km^2) by turtles in different zones versus (2) the size of the zones (km^2), so that the benefit to turtles could be maximized while negative impacts to other stakeholders (e.g. boat operators) could be minimized. In other words, we calculated how much of the 90% kernel area use calculated for each month fell within a conservation zone and divided this value by the size of the conservation zone. So, for example, in May, the 90% kernel area use of the MPA was 2.8 km^2 of Zone A, which is 5.06 km^2 in size, while 5.5 km^2 fell in the proposed zone, which is 5.52 km^2 in size. So, the effectiveness ratio of these two zones in May would be 2.8/5.06 = 0.55 and 5.5/5.52 = 0.99, respectively; so, the proposed zone is 1.8 times more "effective" than Zone A in May.

Results

Breeding seasonality

Male arrival (n = 11 turtles; 2 Jan–11 April; Fig. 2, Table S1a in Appendix 6) to the breeding area began in advance of the onset (3 March) and peak (20–25 April) of mating activity (Fig. 2; Table 1a; n = 94 total mating records). Male departure (n = 42 turtles) began a few days after peak mating, with both departure and mating exhibiting a similar decline into mid-June (correlation coefficient 0.95). Some females arrive at the breeding ground prior to the onset of mating activity (i.e., before early March), with many being present by late April, with the mating season preceding the start of the nesting season by several weeks. However, one female was recorded entering the breeding area as late as 8 June. The first nests by tracked females (n = 37 turtles; 21 May-25 June) closely followed the recorded increase in monitored nesting numbers on the beaches (correlation co-efficient 0.99; Fig. 2; Table S1b in Appendix 6) All tracked females had laid their first clutches before the nesting peak was reached. Females began departing the breeding area (n = 33 turtles; range: 4 July–13 August) after peak nesting, with a similar declining trend in female departure and monitored nesting numbers (correlation-coefficient 0.95; Fig. 2; Table S1b in Appendix 6).

The breeding residency (from arrival to departure) of just four males was recorded, with a mean of 75 days (SD ± 40; range: 30–125). Tracking datasets and photo-identification records confirmed that a minimum of 13 males returned in consecutive years, while long-term tracking showed three males returning to Zakynthos after 2 years, which remained resident at Tunisian and Algerian foraging grounds in the intervening year (based on GPS records at foraging grounds until August 2011 and photo-id confirmation on return to Zakynthos in 2012). These return rates should be treated with caution, as the dataset is small and biased to males captured on Zakynthos in subsequent years, with data on the other 29 males remaining unconfirmed. The residency of just one female could be determined from arrival to departure (40 days); however, 13 females captured in May and June remained resident for longer (mean: 57 days; SD ± 18; range: 40–101 days). Five turtles, which were tracked from before the onset of nesting had enough GPS locations to confirm laying 3 (n = 3) and 4 (n = 2) clutches. All other females (n = 57) were confirmed to lay a minimum of 1-3 clutches. For 30 turtles, the mean internesting period (based on 1-3 definite intervals) was 17 days (SD ± 2;

range: 13–22 days), with estimates ranging from 16-23 days for a further 12 turtles. For more details see the Supplementary Results and Table S1 in Appendix 6.

Home range analysis

In total, 1943 GPS locations were obtained for 35 males and 721 GPS locations were obtained for 28 females at Zakynthos (Fig. 3, Table S2 and Fig S1 in Appendix 6). Information was available for males in all months of the year; however, the sample size was < 10 males in all months, except May (> 30 males). Therefore, trends in area use during individual winter months are presented, but only analyzed in combination with other months (Fig S1 in Appendix 6). Tracking data was only available for females from May to August; however, August had data from a single female (< 10 total daily locations; Fig S1 in Appendix 6) that was only analyzed in combination with other months.

Male area use was primarily focused within the MPA from January to June (>98% locations in the 50% core area of Zones A–C; Table S2 Appendix 6), which is mostly before legislation is in effect (i.e. from May to October). In late-May/early-June, migrants departed the island, while residents dispersed to disparate foraging grounds around the island (Fig. 3ab; Fig. S1 in Appendix 6). The 50% core area in the MPA was primarily divided between the two lesser protected zones from January to June (Zone B: mean 44%; SD ± 14; Zone C: mean 49%; SD ± 14), with negligible activity in Zone A at any time of year. This trend was generally reflected by the 90% home range area. In comparison, 50% and 90% female kernel area use was primarily concentrated in Zone B (Fig. 3c; mean 64% ± 10 and 47% ± 10, respectively); with the other two zones representing 15–18% area use. However, there was a noticeable shift in area use from May to June/July at the onset of nesting activity, with the 50% and 90% home range area of Zone A changing from 8-21% and 11-21%, respectively. Female 50% and 90% home range area outside of the MPA was < 1% and 12% from May to July. In comparison, resident male 50% and 90% home range area outside of the MPA was 24% ± 14 and 44% ± 25, respectively, from July to December.

Optimization of MPA design

Overall, 76% of all locations recorded in the MPA over a 12 month period were encompassed by the existing area (zones A, B and C) and timing (May-October) of

zoning; however, 90% of these locations fell in zones B and C, which receive minimal protection (i.e. boating speed and mooring regulations). The 50% core area use of the breeding population (all turtles combined, males and females separately) occurred along a 5.8 km central coastal stretch of zones B and C in the MPA, and extended 0.5–1.3 km from shore (Fig. 3). Three new zones were tested, which captured between 50% and 96% of sea turtle core area use, and were based on static features (i.e. bathymetry and current zone boundaries for easy implementation; Fig. S2 in Appendix 6). Male and female core area use overlapped along 5.4 km of this central stretch, with greater male use in the western section and greater female use in the eastern section, showing its robustness for incorporation into a zone of maximum protection. Therefore, we investigated the placement of a 7 km by 1 km nearshore zone along this central coastal section (primarily following the 10 m isobath), providing three alternative designs based on bathymetry and existing zoning demarcation (Fig. 4a; Fig. S2 in Appendix 6). The overall effectiveness of these zones was almost identical (max 3% difference for any timing combination; $F_{crit(2,15)} = 0.98$, $P > 0.05$), as the core area used by all turtles (i.e. 50% Kernel of all turtles) was encompassed by all three designs (Fig. 4a presents the example of design 2).

Modifying the existing national park management measures by introducing a more tightly regulated nearshore coastal zone would encompass 72% of all turtle GPS locations recorded in the MPA, thus maximizing turtle protection. The index of effectiveness (Fig. 4b; i.e. the 90% home range area of each month divided by the size of the conservation zone) clearly showed that Zone A (no-use zone) was highly effective (over 90%) during June and July (i.e. when female turtles are nesting), but not at any other time of year (< 20%). In comparison, the large size of Zones B and C meant that their effectiveness was generally low (27–68%); however, the introduction of the nearshore zone of maximum protection (approx. 7 km length by 1 km width, to the < 10 m isobath) that traversed these two lesser-protected zones, indicated that its implementation would prove highly effective (> 90%) at protecting the 90% home range area use by turtles in this population for 9 months of the year, and over 60% effectiveness in the remaining 3 months. Furthermore, this zone could be used to implement additional measures that would enhance the protection of the population in this high use area (i.e. by restricting the types of sea traffic using this zone).

Discussion

This study highlights the importance of assimilating evidence-based information about the temporal and spatial trends of key endangered migratory species (such as sea turtles, in the current case), so that, where possible, coastal MPAs may be designed to maximize protection effort while minimizing the negative impacts on other stakeholders (e.g. wildlife-watching operators, fishermen). Tracking > 100 individuals clearly demonstrate that this loggerhead population migrates into the breeding area several months before seasonal legislation is enforced, and that the strength of existing zoning is not representative of actual area use. Hence, MPA design could be improved by introducing a more tightly regulated nearshore coastal zone that traverses the existing lesser (buffer) protected zones, without enlarging the actual "footprint" of the national park, but which maximally protects the core area used by turtles. By making only a small amendment to the existing MPA design, the national park would result in a large improvement to the conservation planning benefit of the marine area.

MPA design involves many considerations, such as size, timing, zoning, target species coverage, social costs/benefit, economic viability (i.e. cost of enforcing), and flexibility (Agardy *et al.* 2011; Hooker *et al.* 2011; Maxwell *et al.* 2011; Scott *et al.* 2012). Furthermore, regular reassessment and information transfer to management authorities is vital to ensure the appropriate updating of policies (Pullin *et al.* 2004; Sutherland *et al.* 2004; Day 2008). Hence, in recent years, several modeling techniques have been developed to evaluate MPA design, including Marxan, General additive models (GAMs), state-space models and multi criteria evaluation analyses, which evaluate different combinations of parameters including areas of high density use by species, habitat characteristics, seasonality of use and economic costs and benefits (Wood and Dragicevic 2007; Watts *et al.* 2009; Hooker *et al.* 2011; Embling *et al.* 2012). In the current study, we used GIS as a decision support tool to (1) assess the effectiveness of an existing coastal MPA in protecting an endangered sea turtle population, and (2) propose changes to the timing and zoning (Booth 2000; Theobald 2003). Our dataset was primarily assimilated from GPS loggers and Fastloc GPS transmitters attached to sea turtles, the robustness of which has been validated by Hoenner *et al.* (2012) for measuring fine scale spatial behavior of species habitat use.

While MPA design based on a single-species approach is often criticized (Gerber *et al.* 2003), our study further highlighted the complex issues associated with meeting the requirements of one species (Babcock *et al.* 2005; Taylor *et al.* 2007; Hooker *et al.* 2011). For instance, the Zakynthos sea turtle breeding population exhibited dynamic habitat requirements, as well as differences in the timing of migration to and from the MPA. Male habitat use of the area included mating activity in spring (i.e. from early March to June) and foraging activity by year-round residents (in addition to "transient" males from other populations; Casale *et al.* in press) throughout the summer and winter. In comparison, female habitat use of the area included mating activity in the spring and nesting (egg-laying on specific beaches) activity during the summer. As a result, both groups exhibited noticeable shifts in habitat use between May and June; males shifted use from the central MPA ("buffer" zones B–C; mating by both residents and migrants) to the wider island (foraging by residents). In parallel, females shifted use from the central MPA (zones B–C) to the eastern MPA ("core" zone A), where 70% of nesting effort occurs (Schofield *et al.* 2007). Despite these recorded shifts, spatial core habitat requirements remained temporally consistent. This is because, while the most important female nesting beach habitats occur in the eastern part of the MPA (zone A), the central section (zone B–C) is critical for pre- and inter-nesting egg maturation, as the sea temperature of the breeding area remains sub-optimal until July (Schofield *et al.* 2009b; Fossette *et al.* 2012). Therefore, the current study clearly demonstrates the importance of collecting evidence-based information about all components of a given population to identify optimal areas for MPA protection (Pullin *et al.* 2004; Sutherland *et al.* 2004).

Like many MPAs worldwide (Thompson *et al.* 2000), the maritime zoning of the National Marine Park of Zakynthos was based on precautionary measures. The "core" zone (zone A, all boating activity prohibited) was designated based on sea turtle nesting effort, and is adjoined by two lesser protected "buffer" zones (zones B and C, boating activity permitted), and are seasonally implemented from May to October. However, the current study clearly confirmed a mismatch in both the area set aside for core protection and timing of seasonal legislation (Agardy *et al.* 2011). Some studies state that uniform year-round zoning is the most ideal framework for MPA design (Al-Abdulrazzak and Trombulak 2012); yet other studies have shown that enlarging MPAs, particularly buffer zones, does not necessarily enhance their effectiveness (Claudet *et al.* 2008). The coastal MPA of Zakynthos supports both mass tourism and commercial fishing; hence,

zoning is necessary to incorporate the interests of stakeholders and encourage compliance (Halpern *et al.* 2008; Agardy *et al.* 2011), which in turn might also facilitate swift governmental authorization (Togridou *et al.* 2006; Osmond *et al.* 2010; McCay and Jones 2011). Therefore, we evaluated the effectiveness of existing and proposed zoning by quantifying sea turtle space use versus total area under protection for different months of the year. We found that Zone A is highly effective in June and July (as expected, during peak nesting), and may provide additional benefits to offspring that hatch and enter the sea until mid-October; however, the effectiveness of Zones B and C are currently limited. Yet, by introducing a zone of maximal protection in the nearshore area of these two zones, area use by turtles could be optimally protected year-round, while providing economic benefits to the local community. For instance, (1) fishing activity would only be prohibited from 15% of the total available MPA area in winter, (2) the risk of boat-strike to tourists using the nearshore waters in summer (> 500,000) would be reduced, and (3) designating part of this zone to regulated wildlife-watching activities would generate more income to this industry. However, it should be kept in mind that fisheries yield is not only a "surface cover" approach, as fish distribution is regulated by habitat type. For instance, Neptune's seagrass (*Posidonia oceanica*) harbors many fish species targeted by fishermen, but even the largest proposed new zone in this study would only overlap with < 9% of this habitat type within the protected marine area (Pasqualini *et al.* 2005), as this zone primarily covers unvegetated habitats. Overall, the suggested new zone (which to a certain degree has already been discussed at a preliminary phase with professional wildlife-watching boat owners based on data assimilated by Schofield *et al.* 2004; 2007) would facilitate the management of the sea turtle population, redistributing protective effort to the central nearshore area, while simultaneously retaining the existing MPA boundaries (Babcock *et al.* 2005; Scott *et al.* 2012). It is important to retain these existing boundaries (timing and zoning), as the MPA also safeguards other species (such as the critically endangered Mediterranean monk seal, *Monachus monachus*) and habitats (such as Neptune's seagrass, *P. oceanica*), for which information must be assimilated to implement an ecosystem approach to improve the design of this MPA in the future.

Our study provides evidence that males primarily return annually to this breeding area, as opposed to females that tend to return biannually, further supporting our previous studies with more limited sample sizes (Hays *et al.* 2010; Schofield *et al.* 2010a).

Because males return more frequently to breed than females, it is important to ensure that they are adequately protected during residency at Zakynthos. Furthermore, a study by Casale *et al.* (2012) showed that turtles from other areas may use the Zakynthos MPA in winter. We also show that migratory males may remain resident for up to 125 days, while females may remain even longer, as mating activity has been recorded from March onwards. Our finding of sea turtle mating preceding the nesting season has also been shown for other populations (Godley *et al.* 2002; Henwood, 1987); however, the number of females that arrive at the breeding grounds before they actually start mating is not known. Hence, it is extremely important to develop an understanding of the energetic expenditure of males and females (Fossette *et al.* 2012), and to determine whether recreational marine activities or commercial fishing activity impact reproductive fitness/output (Southall *et al.* 2006), including the clutch frequency and clutch size of females. Such fine-scale studies of sea turtle reproductive fitness in relation to anthropogenic activities would provide a basis on which to further refine regulations within the existing and suggested zones (Babcock *et al.* 2005; Agardy *et al.* 2011).

Information is not currently available to evaluate the overlap in sea turtle watching or fishing activities with sea turtle habitat use. Furthermore, habitat use by resident males beyond the MPA was not assessed, as their numbers (< 7 individuals) were not representative at the population level (Borger *et al.* 2006; Murray 2006; Lindberg and Walker 2007; Schofield *et al.* in press). Photographic records assimilated by the lead author during photo-identification research (n = 493 turtles, representing an estimated 50% of the breeding population; Schofield et al., 2008, 2009a) indicate that over 40% of turtles frequenting the NMPZ area have sustained some sort of physical injury from human activities (boat strike or fishing gear), while strandings (i.e., injured or dead turtles washed ashore) on the island also provide evidence of this; however, in both instances the actual site of trauma is unknown. Therefore, at present, the most pragmatic way to gauge the potential impact of various human activities in the marine environment is to track their movement patterns, as with turtles, and identify areas where there is an overlap. This has similarly been done for whale versus commercial shipping vessels in northern latitudes (Williams and O'Hara, 2010). Our results from the current study indicate that governance activities should focus on enforcing existing zoning legislation until more information about other species and habitats of importance

has been collected, and introducing a new tightly regulated zone that targets core area use by the breeding population to enhance protection effort. This pragmatic amendment to the existing MPA would both maximize sea turtle protection while minimizing the negative impacts on other stakeholders (e.g., wildlife-watching vessels and fishermen). In conclusion, this study demonstrates the importance of (1) understanding the habitat requirements of all components in a given population, (2) using evidence-based information to improve the delineation and timing of MPAs originally based on precautionary measures, and (3) regularly reassessing existing policies and anthropogenic activities to ensure optimal MPA structuring.

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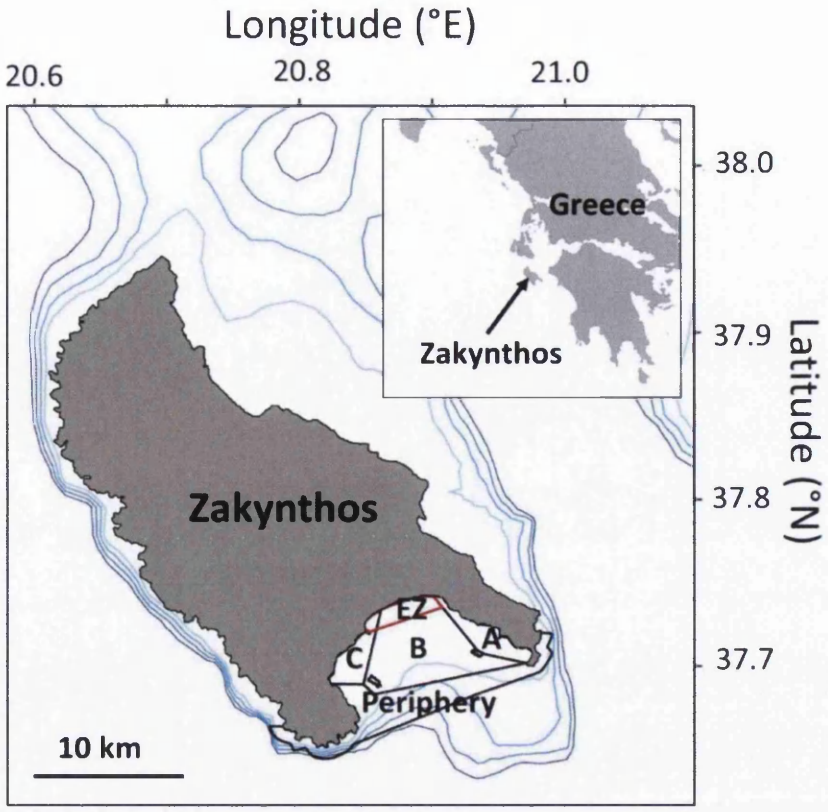

Fig. 1. Map of Zakynthos (with insert showing the location of the island in Greece). National Marine Park of Zakynthos maritime zones are shown, in addition to the previously suggested NMPZ Ecotourism zone (EZ) to improve turtle protection and the regulation of turtle watching activity. Protective legislation is in place from May to October only. Maritime Zone A = no sea vessels permitted; Maritime Zone B = sea vessels permitted at 6 $km.h^{-1}$ but no mooring; Maritime Zone C = sea vessels permitted at 6 6 $km.h^{-1}$ and mooring. Island bathymetry contours (i.e. 50, 100, 150, and 200 m) were extracted from the ETOPO1 1 arc-minute global relief model (Amante *et al.* 2009).

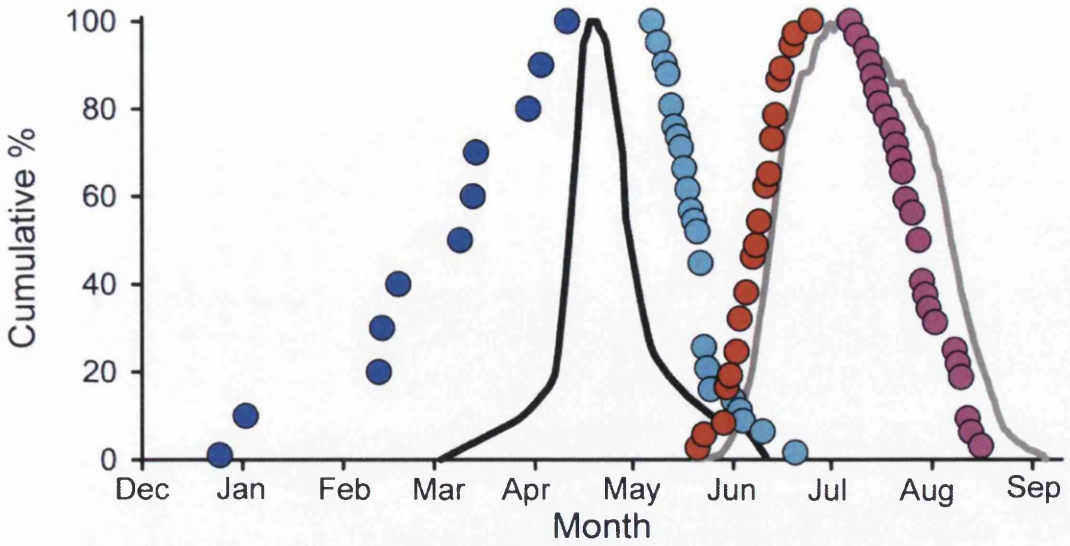

Fig. 2. Cumulative percentages showing male arrivals (n = 11, blue circles) and departures (n = 42, turquoise circles), female first nesting (n = 37, red circles) and departures (n = 32, pink circles), mating (n = 94 records, black line) and nesting (n = 1113, 994 and 897 records combined for 2007, 2008 and 2009, respectively grey line) activity. For more details please see Table S1 (Appendix 6).

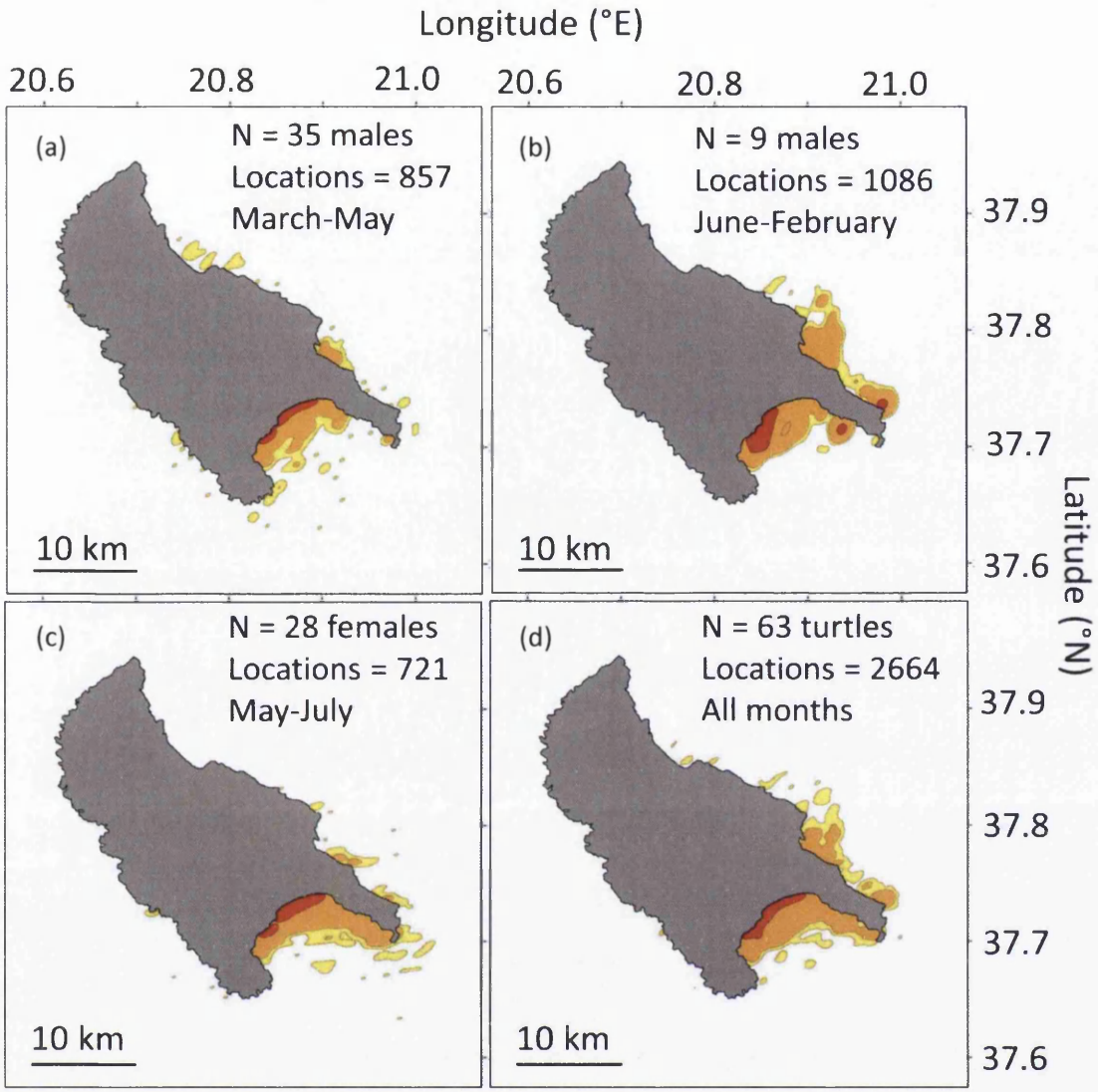

Fig. 3. The 50% (red), 90% (orange) and 95% (yellow) Kernel home range area use of (a) males March to May (i.e. mating period; n = 35 turtles; total daily locations = 857); (b) males June to February (i.e. foraging period; n = 9 turtles; total daily locations = 1086); (b) females May to July (i.e. breeding period; n = 28 turtles; total daily locations = 721); (d) all male and female datasets combined (males, n = 35, females, n = 28, total daily locations = 2661). See Table S1 and Fig. S1 (Appendix 6) for a breakdown of home range by month, with the number of turtles and number of points represented in each month. Protective legislation is in place from May to October of each year.

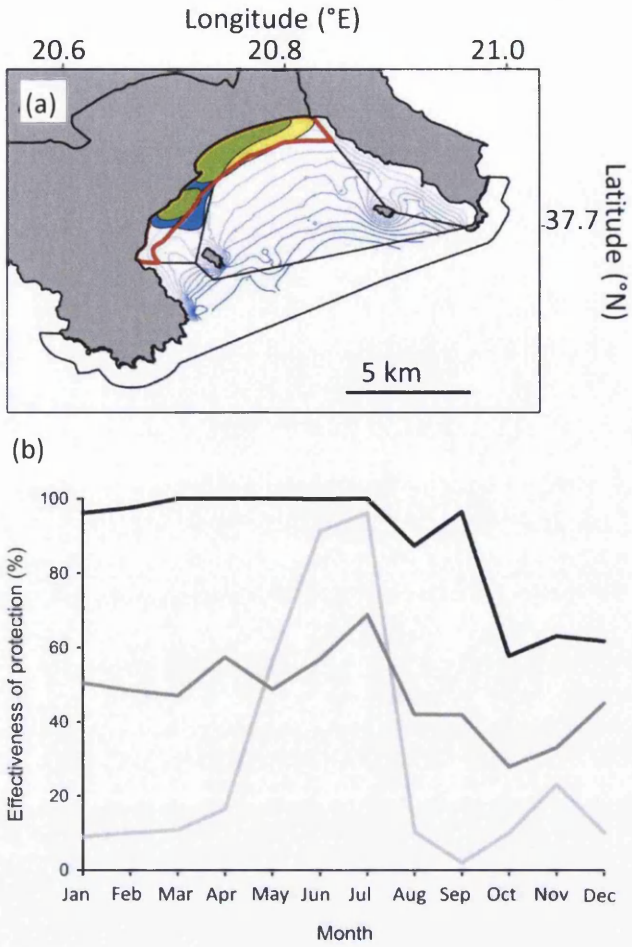

Fig. 4. (a) An example of the proposed zone based on the current study findings to protect the core area use by the breeding population based on the 50% Kernel area for all males (blue), all females (yellow) and both sexes combined (green). Existing zoning and bathymetry at 5 m isobaths intervals is shown. This protection zone primarily follows the 10 m isobath for ease of implementation. (b) The index of "effectiveness to evaluate the suitability of the existing (Zone A = light grey line; Zones B and C combined = dark grey line) and proposed (black line) conservation zones based on (1) the 90% GIS home range area use (i.e. total home range area; km^2) by turtles in different zones versus (2) the size of the zones (km^2), so that the benefit to turtles could be maximized while negative impacts to other stakeholders (e.g., boat operators) could be minimized. In other words, we calculated how much of the 90% home range area calculated for each month fell within a conservation zone and divided this value by the size of the conservation zone. We combined the two lesser protected zones B and C for this analysis for comparison with the proposed zone, which overlays the nearshore section of both zones, and because both produced almost identical results (data not shown). This graph clearly indicates that the proposed zone (narrow stretch of nearshore waters, 7 by 1 km, overlaying Zones B and C) should be implemented year-round, while the existing zoning (A, B and C) should continue to be implemented from May to October.

Table 1a. Assimilated mating information spanning 2003-2012.

Year	Mating events (Total)	Last event	First mating	Peak event
2003–2012	94	3 March	16–24 April	13 June

Table 1b. Nesting information obtained during daily NMPZ nesting beach surveys from 2007-2009. "Regular nesting" indicates the period when nests were recorded on every consecutive day.

Year	Total nest (n)	1st Nest of season	Onset of regular nesting	Mean date of nesting	Nesting peak	End of regular nesting	Last nest of season
2007	1113	17 May	1 June	3 July	27 June	5 Aug	1 Sept
2008	994	29 May	1 June	4 July	11 July	5 Aug	25 Aug
2009	857	25 May	2 June	7 July	12 July	13 Aug	10 Sept

Appendix 6

Supplementary results

The mean curved carapace length (CCL) of male loggerheads was 82.9 cm (n = 45, SD ± 7, range: 71–102 cm), while that of females was 83.9 cm (n = 63, SD ± 4.5, range: 74–96 cm) (Table S1). Migratory males and residents to the island outside of Laganas Bay returned to the breeding area between January and April (n = 11 turtles; mean: 2 March; SD ± 29; range: 2 Jan–11 April; Fig. 2; Table S1a), with one transient male being present from December to February (Casale *et al.* 2012). Migratory males departed the breeding area at the end of May (n = 33 turtles; mean: 19 May; SD ± 6; range: 7 May–4 June; Fig. 2; Table S1a), whereas residents to other parts of the island remained until mid-June (n = 2; 18 and 20 June; Fig. 2; Table S1a). The breeding residency, from arrival to departure, of just four males was recorded, with a mean of 75 days (SD ± 40; range: 30–125). Tracking datasets and photo-identification records confirmed that at least 14 of the males return in consecutive years, while long-term tracking showed two males remaining resident at Tunisian foraging grounds during the subsequent season, with photo-id confirming their return to Zakynthos in 2012. A further male was tracked remaining resident at an Algerian foraging ground during the subsequent season, with the return rate being unknown. These datasets should be treated with caution due to the small sample size, and bias towards males that were observed on consecutive years at Zakynthos.

The earliest mating activity was recorded on 3rd March (Table 1a); hence, females are likely to begin arriving as early as February. However, only two females have been tracked long enough, with one returning in April (Zbinden *et al.* 2012) and one returning on 8 June (this study). Both turtles returned after 2 years (i.e. 2004-2006 and 2009-2011). Mating activity peaked between the 20–25 April (Table 1b), and then tailed off sharply, with male departure being closely correlated with the decline in observed mating activity (Fig. 2; Correlation coefficient 0.95). The latest mating record was on 13 June.

Based on nesting data the first nest in 2007–2009 was recorded on 23 May (range 17–29 May) and the last nest was recorded on 1 September (range: 25 August–10 September).

The onset and termination of regular nesting (i.e. at least one nest recorded every day) was 1 June and 5 August. Peak nesting ranged from 27 June to 12 July (mean 5 July).

The onset of nesting by tracked females closely followed the increase in nest numbers (correlation co-efficient 0.95), while departures followed the decline in nest numbers immediately after the peak was reached (Fig. 2; correlation co-efficient 0.99). The first clutch laid by females in all years (2006–2011) ranged from 21 May-25 June (n = 37 turtles; mean: 7 June; SD ± 8; Fig. 2; Table S1b). The final clutch laid by females in all years (2004–2011) ranged from 4 July-13 August (n = 33 turtles; mean: 24 July; SD ± 11; Fig. 2; Table S1b). The residency of just one female could be determine from arrival to departure (40 days); however, 13 females remained for longer than this period after initial capture in May and June (mean: 57 days; SD ± 18; range: 40–101 days). Five turtles, which were tracked from before the onset of nesting and with sufficient GPS locations, were confirmed to lay 3 (n = 3 turtles) and 4 (n = 2 turtles) clutches. All other turtles (n = 57 turtles) were confirmed to lay at least 1 clutch or at least 3 clutches (as complete records were not obtained). For 30 turtles, a mean internesting period (based on 1-3 definite intervals) of 17 days was determined (SD ± 2; range: 13–22 days), with estimates ranging from 16-23 days for a further 12 turtles.

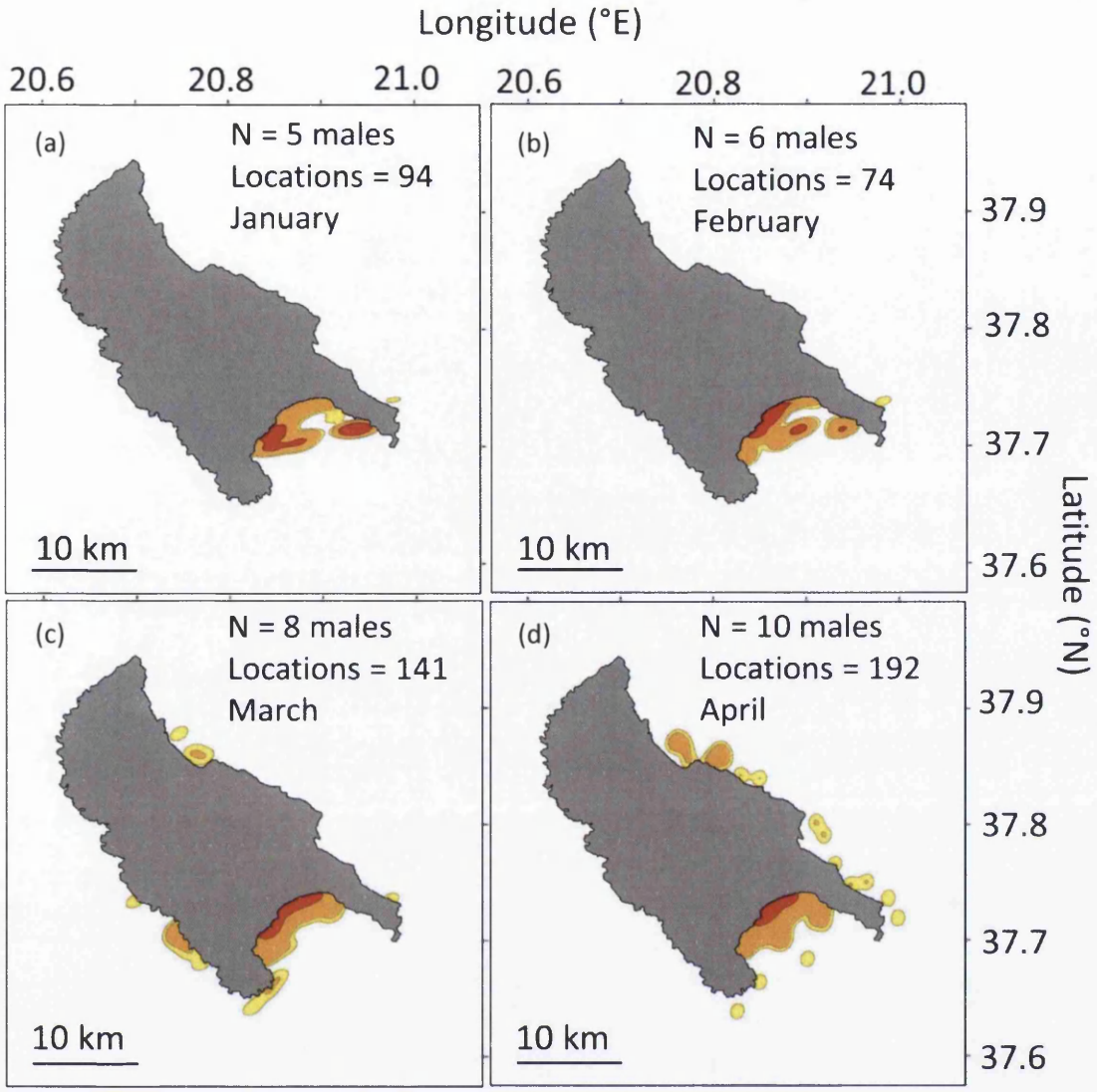

Fig. S1(a-d). The 50% (red), 90% (orange) and 95% (yellow) kernel home range area use by male and female turtles for each month of the year.

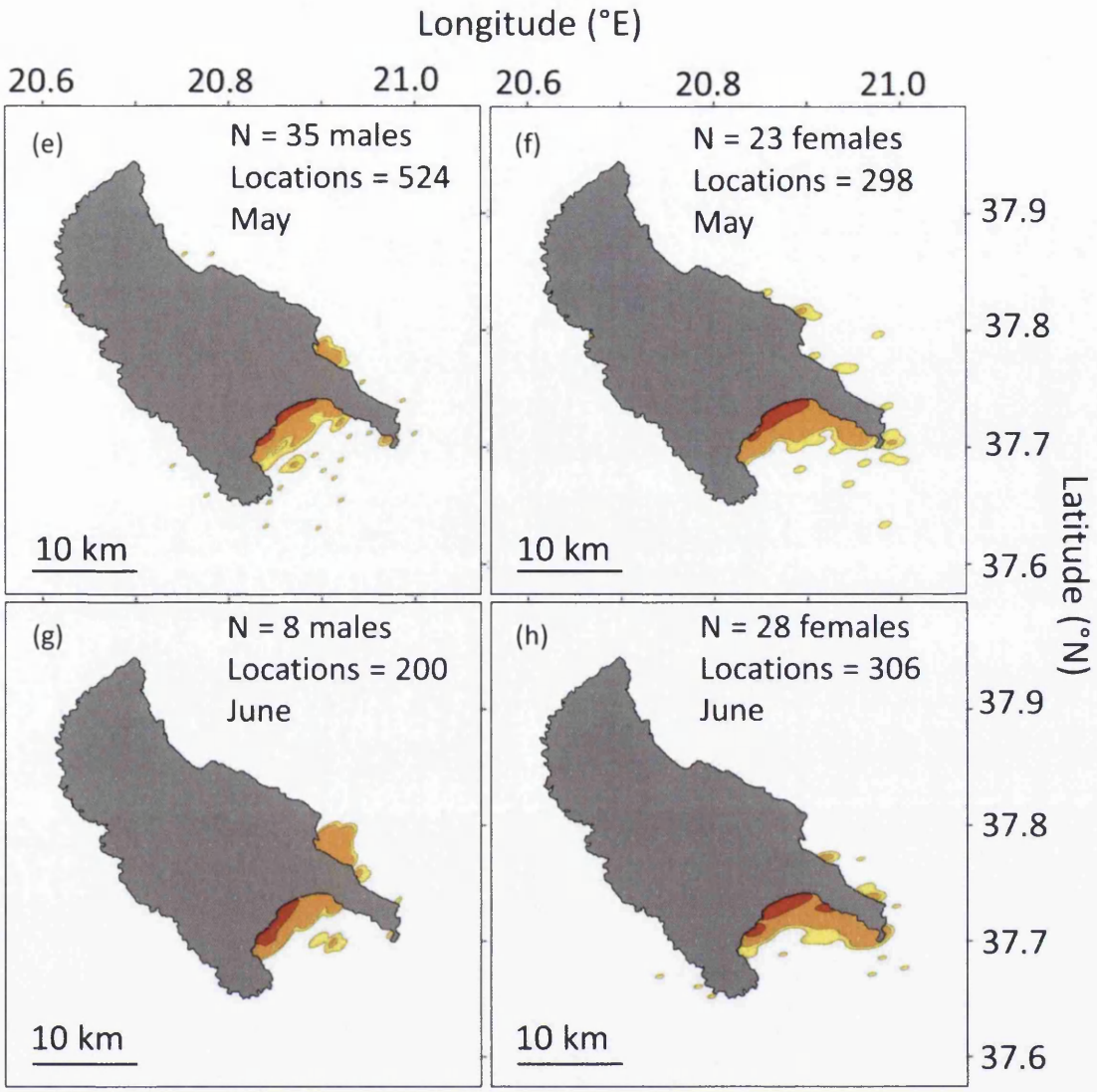

Fig. S1(e-h). The 50% (red), 90% (orange) and 95% (yellow) kernel home range area use by male and female turtles for each month of the year.

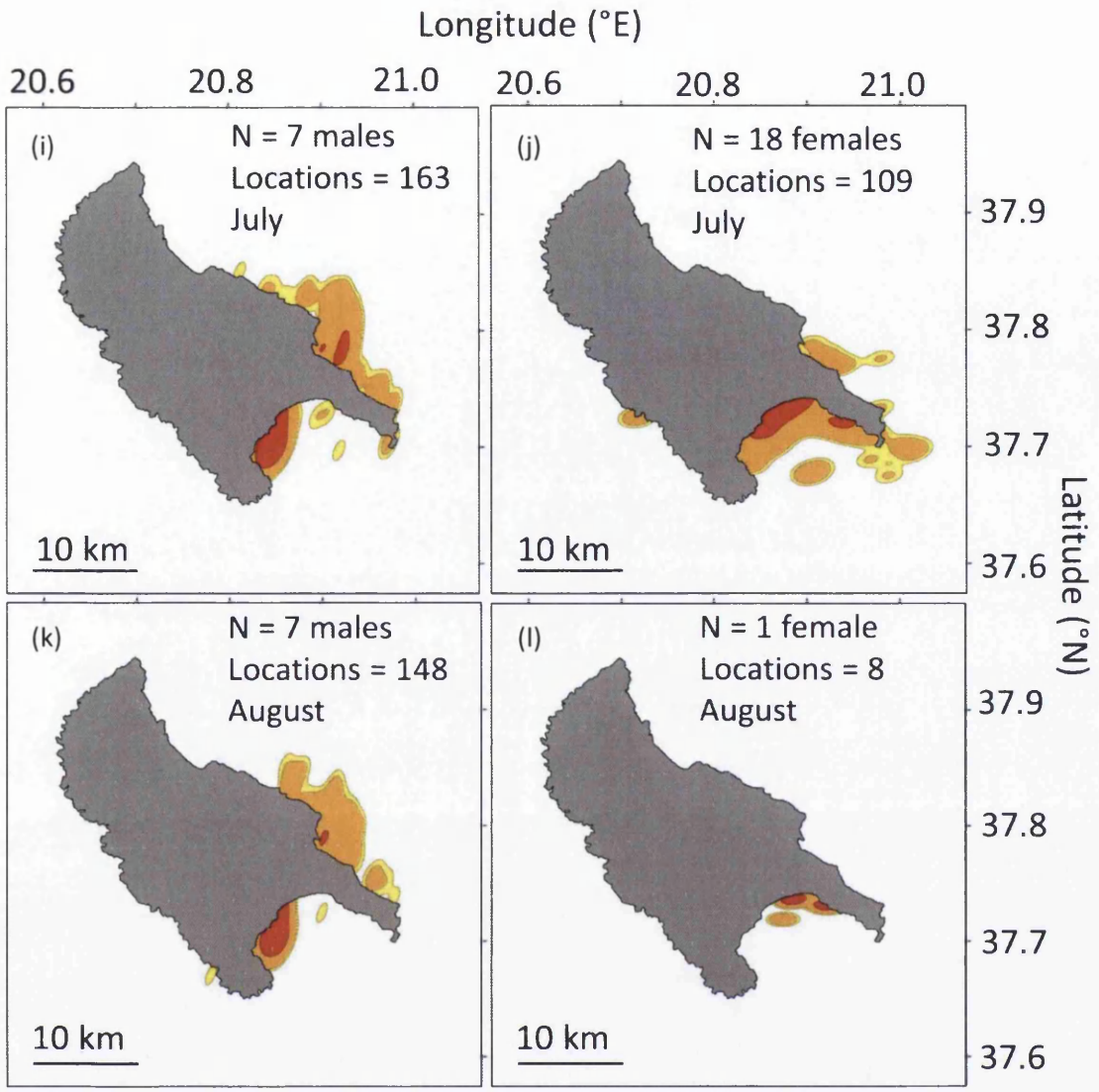

Fig. S1(i-l). The 50% (red), 90% (orange) and 95% (yellow) kernel home range area use by male and female turtles for each month of the year.

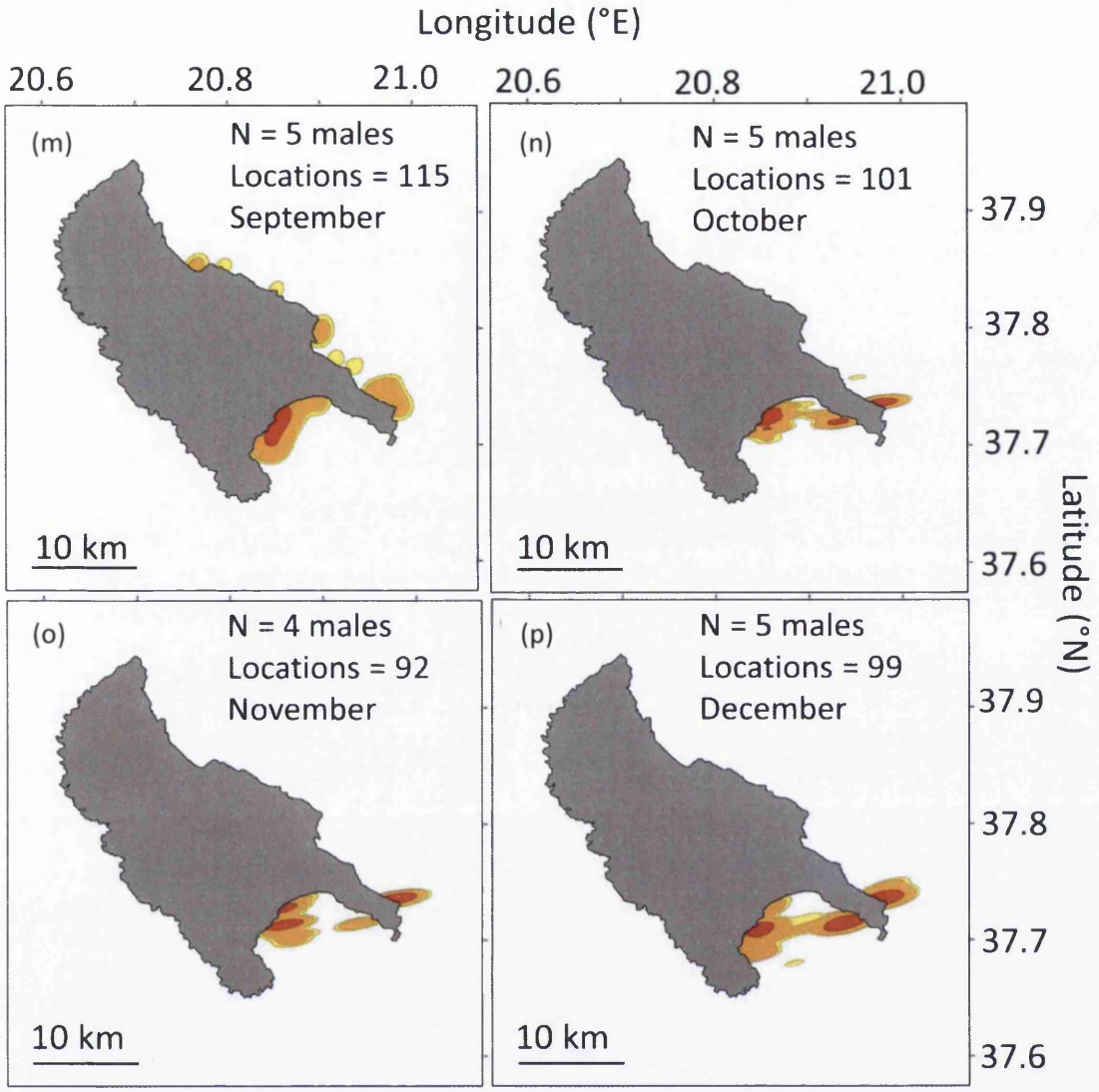

Fig. S1(m-p). The 50% (red), 90% (orange) and 95% (yellow) kernel home range area use by male and female turtles for each month of the year.

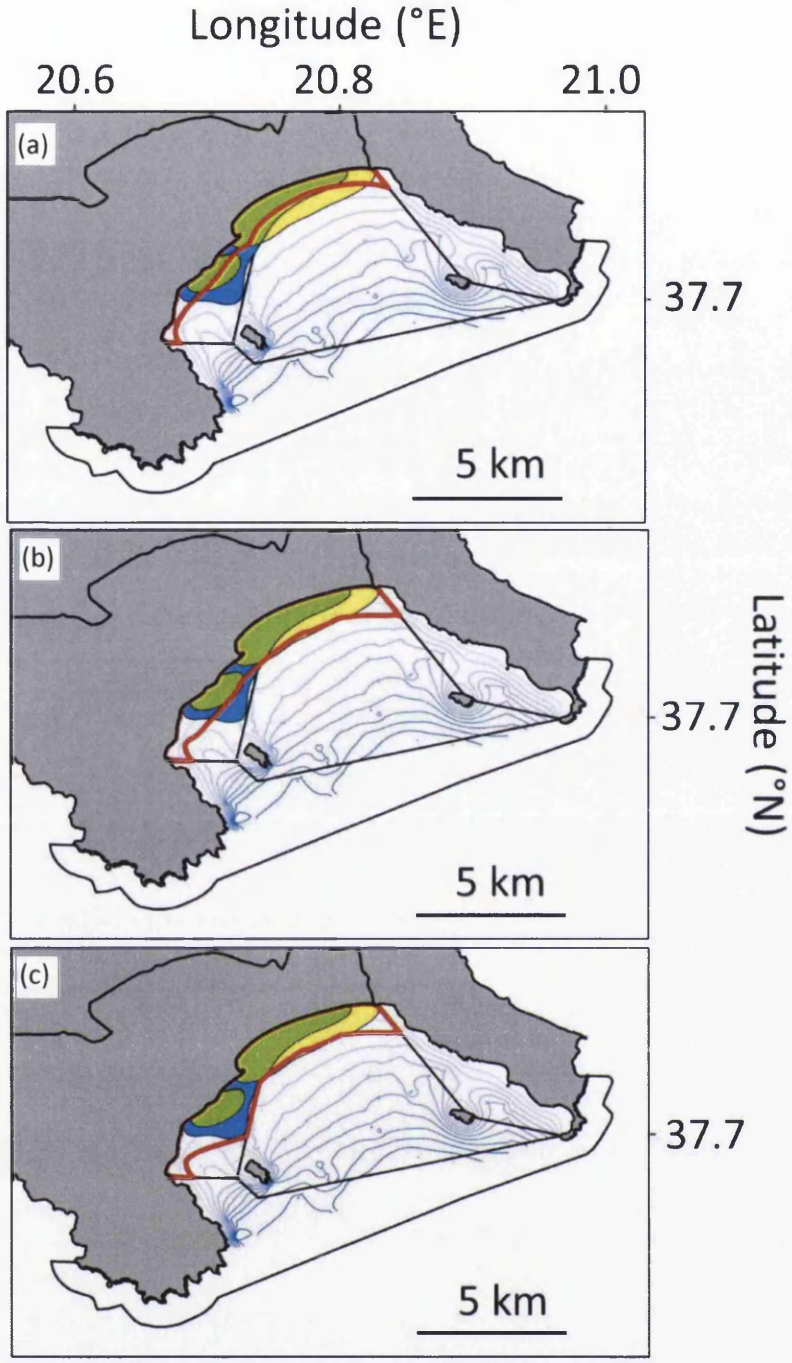

Fig. S2. Proposed zoning designs based on the core area use of turtles indicated by 50% kernel analyses of males (blue), females (yellow) and all turtles combined (green). We suggested three possible designs utilizing the bathymetry and existing zoning demarcation (Supplementary Figure 2a–c): (a) using the 5 m isobaths, which excluded 49% of the three different 50% kernels; (b) using the 10 m isobaths, which excluded 15% of the three different 50% kernels; and (c) using the 10 m isobath and part of the existing zone C, which excluded 4% of the three different 50% kernels. In all cases, we used the east and west limits of Zones A and C, respectively, as fixed points.

Table S1. Deployment details for the 109 tracked turtles: (a) male (n = 46, of which six were tracked for more than one breeding season) and (b) female (n = 63, of which one was tracked for more than one breeding season). Note: all turtles, except males 20, 28 and 41 to 45, were previously published by Schofield *et al.* (2009; 2010ab, in press) and Hays *et al.* (2010). CCL = curved carapace length; (R) = Resident to the breeding area. Information about male 46* was obtained from Casale *et al.* (2012), with the first date indicating arrival to breeding area, not date of attachment. Information about females 1–7 and 17 –27 was obtained from Zbinden *et al.* (2007; 2011). The "Duration (days)" is provided until 31/7/2012.

(a) Males – 1945 locations

Turtle	CCL (cm)	Deployed	Duration (days)	Unit attached	Date unit attached	Date departed breeding area	Date returned to breeding area	Viable data for GIS analysis (no. daily locations)	Return rates (all observed courting/mating)
1	81	2007	49	Sirtrack Fastloc	8/5/2007	n/a (R)	n/a	yes (45)	Annual, 2008–2012 photo-id confirmation
2	91	2007	51	Sirtrack Fastloc	10/5/2007	22/5/2007	n/a	yes (6)	
3	81	2007	3	Sirtrack Fastloc	14/5/2007	14/5/2007	n/a	no (1)	
4	79	2007	17	Sirtrack Fastloc	10/5/2007	23/5/2007	n/a	yes (10)	
5	90	2007	128	Sirtrack - PTT	7/5/2007	23/5/2007	n/a	yes (11)	Annual, 2008–2010 photo-id confirmation
		2009	58	Sirtrack Fastloc	8/5/2009	19/5/2009	n/a	yes (8)	
7	87	2008	364	Sirtrack Fastloc	3/5/2008	22/5/2008	13/2/2009	yes (18)	1 year, 2009, photo-id confirmation
		2009	156	Sirtrack Fastloc	(2/5/2009)	9/5/2009	n/a	yes (76)	
9	80	2008	367	Sirtrack Fastloc	3/5/2008	18/6/2008 (R)	2/1/2009	yes (356)	1 year, 2009, photo-idconfirmation (died 2009)
		2009	102	Sirtrack Fastloc	(5/5/2009)	7/5/2009	n/a		
11	90	2008	367	Sirtrack Fastloc	4/5/2008	24/5/2008	11/4/2009	yes (44)	1 year, 2009, photo id-confirmation, mating
		2009	84	Sirtrack Fastloc	(6/5/2009)	11/5/2009	n/a		

13	78	2008	367	Sirtrack Fastloc	9/5/2008	17/5/2008 (R)	14/3/2009	yes (124)	1 year, 2009, photo id-confirmation, mating
		2009	360	Sirtrack Fastloc	(7/5/2009)	13/5/2009	12/2/2010	yes (344)	1 year, 2010, photo id-confirmation, mating
15	84	2008	64	Sirtrack Fastloc	15/5/2008	1/6/2008	n/a	yes (11)	
16	78	2008	32	Sirtrack Fastloc	16/5/2008	25/5/2008	n/a	yes (10)	
17	90	2009	178	Sirtrack Fastloc	3/5/2009	17/5/2009	n/a	no (1)	1 year, 2010 photo id; then 2012 photo-id
18	98	2009	138	Sirtrack Fastloc	2/5/2011	20/5/2009	n/a	no (2)	
19	78.5	2009	52	SMRU - SRDL	7/5/2009	23/5/2009	n/a	no (0)	No record 2010; Photo-id 2011 and 2012
	79	2012	85	Wildlife Comp	7/5/2012	20/6/2012	n/a	yes (44)	
21	102	2009	88	Sirtrack Fastloc	2/5/2009	24/5/2009	n/a	yes (17)	
22	90.5	2009	11	Sirtrack Fastloc	6/5/2009	n/a	n/a	no (0)	
23	89	2009	60	Sirtrack Fastloc	7/5/2009	9/5/2009	n/a	no (2)	
24	80	2009	368	Sirtrack Fastloc	8/5/2009	20/6/2009 (R)	13/3/2010	yes (367)	1 year, 2010, photo id-confirmation, mating
25	79	2010	142	Sirtrack Fastloc	3/5/2010	16/5/2010	n/a	yes (9)	
26	75.5	2010	479	Sirtrack Fastloc	3/5/2010	15/5/2010	n/a	yes (11)	2 year, 2011 Tunisia GPS, 2012 Zakynthos pho-id
27	85.5	2010	407	Sirtrack Fastloc	3/5/2010	14/5/2010	n/a	yes (11)	2 year, 2011 Tunisia GPS, 2012 Zakynthos pho-id
		2012	89	Wildlife Comp	13/5/2012	23/5/2012	n/a	yes (11)	
29	85	2010	363	Sirtrack Fastloc	8/5/2010	23/5/2010	18/2/2011	yes (52)	1 year, 2011, photo id-confirmation, mating
30	86	2010	349	Sirtrack Fastloc	8/5/2010	25/5/2010	n/a	no (1)	Found dead 2011 at Kefalonia
31	82.5	2010	330	Sirtrack Fastloc	9/5/2010	18/5/2010	n/a	no (2)	2011 summer Algeria, i.e. not annual return rate
32	77.5	2010	75	Sirtrack Fastloc	10/5/2010	13/5/2010	n/a	no (1)	
33	72	2010	50	Sirtrack Fastloc	11/5/2010	12/5/2010	n/a	yes (26)	
34	88	2011	105	Sirtrack Fastloc	4/5/2011	21/5/2011	n/a	yes (11)	
35	73	2011	161	Sirtrack Fastloc	6/5/2011	23/5/2011	n/a	yes (11)	
36	83.5	2011	331	Sirtrack Fastloc	7/5/2011	23/5/2011	9/3/2012	yes (40)	1 year, 2012, photo id-confirmation

37	72.5	2011	109	Sirtrack Fastloc	8/5/2011	19/5/2011	n/a	yes (6)	
38	71	2011	363	Sirtrack Fastloc	9/5/2011	n/a (R)	3/4/2012	yes (189)	1 year, 2012, photo-id confirmation
39	83	2011	359	Sirtrack Fastloc	13/5/2011	23/5/2011	30/3/2012	yes (40)	1 year, 2012, photo id-confirmation
40	76	2011	104	Sirtrack Fastloc	14/5/2011	4/6/2011	n/a	yes (19)	
41	88	2012	87	Sirtrack Fastloc	5/5/2012	22/5/2012	n/a	yes (18)	
42	82	2012	86	Sirtrack Fastloc	6/5/2012	3/6/2012	n/a	yes (25)	
43	77	2012	86	Sirtrack Fastloc	6/5/2012	11/5/2012	n/a	yes (5)	
44	90	2012	80	Sirtrack Fastloc	12/5/2012	13/5/2012	n/a	no (1)	
45	85	2012	85	Wildlife Comp	7/5/2012	18/5/2012	n/a	yes (10)	
46*	85	2006	n/a	Telonics-PTT	25/12/2006	25/2/2007	n/a	n/a	

(b) Females – 729 locations

Turtle	CCL (cm)	Deployed	Duration (days)	Unit	Date unit attached	Date departed breeding area	Date returned to breeding area	First nest	Last nest	Total nests recorded	Internesting interval (days)	Viable data for GIS analysis (no daily locations)
1	85	2004	124	Sirtrack Kiwisat	28/6/2004	11/8/2004	n/a	n/a	10/8/2004	min 3	est. 21	no (0)
2	86	2004	124	Sirtrack Kiwisat	29/6/2004	24/7/2004	spring, 2006	n/a	23/7/2004	min 2	est. 23	no (0)
3	91	2004	135	Sirtrack Kiwisat	30/6/2004	10/8/2004	n/a	n/a	9/8/2004	min 3	est. 20	no (0)
4	79	2005	95	Sirtrack Kiwisat	17/6/2005	29/7/2005	n/a	n/a	28/7/2005	min 3	est. 20	no (0)
5	87	2005	110	Sirtrack Kiwisat	20/6/2005	27/7/2005	n/a	n/a	26/7/2005	min 3	est. 18	no (0)
6	89	2005	120	Sirtrack Kiwisat	22/6/2005	8/8/2005	n/a	n/a	7/8/2005	min 3	est. 23	no (0)
7	76	2005	93	Sirtrack Kiwisat	10/8/2005	10/8/2005	n/a	n/a	9/8/2005	min 1	n/a	no (0)
8	81	2006	19	TrackTag /Lotek	19/5/2006	n/a	n/a	31/5/2006	n/a	min 1	n/a	yes (19)
9	89	2006	32	TrackTag/Lotek	23/5/2006	n/a	n/a	25/6/2006	n/a	min 1	n/a	yes (32)
10	87	2006	25	TrackTag/Lotek	24/5/2006	n/a	n/a	7/6/2006	n/a	min 2	19	yes (25)
11	85.5	2006	34	Lotek TDR	16/5/2006	n/a	n/a	2/6/2006	n/a	min 2	17	n/a
12	81	2006	50	Lotek TDR	25/5/2006	n/a	n/a	12/6/2006	n/a	min 3	17; 15	n/a
13	n/a	2006	16	Lotek TDR	4/7/2006	n/a	n/a	19/6/2006	n/a	min 2	16	n/a
14	86	2007	112	Telonics A-2010	9/7/2007	26/7/2007	n/a	n/a	25/7/2007	min 2	16	no (0)
15	86	2007	316	Telonics A-2010	10/7/2007	25/7/2007	n/a	n/a	24/7/2007	min 2	14	no (0)
16	82	2007	60	Telonics A-2010	11/7/2007	28/7/2007	n/a	n/a	27/7/2007	min 2	16	no (0)
17	85	2007	59	Telonics A-2010	11/7/2007	12/7/2007	n/a	n/a	11/7/2007	min 1	n/a	no (0)
18	79	2007	427	Telonics A-2010	12/7/2007	13/7/2007	n/a	n/a	12/7/2007	min 1	n/a	no (0)
19	88	2007	117	Telonics A-2010	13/7/2007	14/7/2007	n/a	n/a	13/7/2007	min 1	n/a	no (0)

20	87	2007	96	Telonics A-2010	17/7/2007	18/7/2007	n/a	n/a	17/7/2007	min 1	n/a	no (0)
21	76	2007	85	Telonics A-2010	20/7/2007	21/7/2007	n/a	n/a	20/7/2007	min 1	n/a	no (0)
22	89	2007	134	Sirtrack Kiwisat	21/7/2007	6/8/2007	n/a	n/a	5/8/2007	min 2	15	no (0)
23	82	2007	220	Sirtrack Kiwisat	25/7/2007	10/8/2007	n/a	n/a	9/8/2007	min 2	15	no (0)
24	78	2007	672	Telonics A-2010	26/7/2007	27/7/2007	n/a	n/a	26/7/2007	min 1	n/a	no (0)
25	83	2007	52	TrackTag/Lotek	4/5/2007	n/a	n/a	5/6/2007	n/a	min 2	20	yes (49)
26	84	2007	34	TrackTag/Lotek	8/5/2007	n/a	n/a	3/6/2007	n/a	min 1	n/a	yes (33)
27	81	2007	62	TrackTag/Lotek	9/5/2007	n/a	n/a	21/5/2007	n/a	min 3	22; 16	yes (36)
28	77	2007	35	TrackTag	11/5/2007	n/a	n/a	23/5/2007	n/a	min 2	19	yes (34)
29	87	2007	34	Cefas G5	16/5/2007	n/a	n/a	2/6/2007	n/a	min 2	17	n/a
30	79.5	2007	37	Cefas G5	16/5/2007	n/a	n/a	14/6/2007	n/a	min 1	n/a	n/a
31	82	2007	28	Cefas G5	16/5/2007	n/a	n/a	13/6/2007	n/a	min 1	n/a	n/a
32	78	2008	233	Sirtrack Fastloc	15/5/2008	22/7/2008	n/a	31/5/2008	21/7/2008	est. 4	est. 17	yes (21)
33	90	2008	280	Sirtrack Fastloc	24/5/2008	6/8/2008	n/a	29/5/2008	5/8/2008	est. 4	est. 18	yes (10)
34	88	2008	131	Sirtrack Fastloc	24/5/2008	16/7/2008	n/a	15/6/2008	n/a	min 3	est. 18	yes (10)
35	88.5	2008	88	Sirtrack Fastloc	23/5/2008	19/7/2008	n/a	3/6/2008	18/7/2008	est. 3	17; 21	yes (29)
36	82	2008	22	Sirtrack Fastloc	23/5/2008	n/a	n/a	5/6/2008	n/a	min 2	21	yes (14)
37	78	2008	272	Sirtrack Fastloc	24/5/2008	10/7/2008	n/a	8/6/2008	9/7/2008	3	16; 14	yes (27)
38	83	2008	3	Sirtrack Fastloc	24/5/2008	n/a	n/a	n/a	n/a	n/a	n/a	n/a
39	84	2008	42	TrackTag/CefasG5	8/5/2008	n/a	n/a	14/6/2008	n/a	min 2	15	yes (40)
40	84	2008	36	TrackTag	8/5/2008	n/a	n/a	14/6/2008	n/a	min 1	n/a	yes (29)
41	88	2008	35	TrackTag	8/5/2008	n/a	n/a	13/6/2008	n/a	min 1	n/a	yes (17)
42	86	2008	38	TrackTag/CefasG5	6/5/2008	n/a	n/a	20/6/2008	n/a	min 1	n/a	yes (33)
43	86.5	2008	46	TrackTag	8/5/2008	n/a	n/a	8/6/2008	n/a	min 2	17	yes (43)

44	88.5	2008	32	TrackTag	9/5/2008	n/a	n/a	11/6/2008	n/a	min 1	n/a	yes (14)
45	80	2008	38	TrackTag/CefasG5	9/5/2008	n/a	n/a	16/6/2008	n/a	min 1	n/a	no (0)
46	85.5	2009	145	Sirtrack Fastloc	5/5/2009	14/8/2009	n/a	12/6/2009	13/8/2009	4	21; 19; 17	yes (26)
47	80	2009	41	Sirtrack Fastloc	29/6/2009	20/7/2009	n/a	n/a	21/7/2009	min 2	est. 17	yes
48	88.5	2009	707	Sirtrack Fastloc	29/6/2009	26/7/2009	n/a	n/a	27/7/2009	min 3	est. 16	yes (11)
49	82.5	2009	104	Sirtrack Fastloc	30/6/2009	11/7/2009	n/a	n/a	10/7/2009	min 1	n/a	yes (6)
50	83	2009	101	Sirtrack Fastloc	29/6/2009	5/7/2009	n/a	n/a	4/7/2009	min 1	n/a	no (3)
51	80	2009	60	Sirtrack Fastloc	30/6/2009	27/7/2009	n/a	n/a	26/7/2009	min 3	est. 16	yes (11)
52	74.5	2009	1109	Sirtrack Fastloc	18/7/2009	31/7/2009	8/6/2011	n/a	30/7/2009	min 2	13	no (3)
		2011		Sirtrack Fastloc	n/a	18/7/2011	n/a	9/6/2011	14/7/2011	3	19; 17	yes (29)
54	88	2009	26	Sirtrack Fastloc	20/7/2009	7/8/2009	n/a	n/a	6/8/2009	min 2	17	yes (5)
55	82	2009	460	SMRU GPS-GSM	2/5/2009	7/7/2009	n/a	29/5/2009	6/7/2009	3	19; 18	yes (50)
56	90	2009	72	SMRU GPS-GSM	3/5/2011	n/a	n/a	30/5/2009	n/a	min 3	21; 17	yes (46)
57	83.5	2009	156	SMRU Solar	8/5/2009	22/7/2009	n/a	5/6/2009	21/7/2009	4	18; 15; 13	yes (11)
58	85	2010	40	Cefas G6	9/5/2010	n/a	n/a	2/6/2010	n/a	min 2	16	n/a
59	90	2010	46	Cefas G6	10/5/2010	n/a	n/a	9/6/2010	n/a	min 2	16	n/a
60	78	2010	46	Cefas G6	11/5/2010	n/a	n/a	9/6/2010	n/a	min 2	17	n/a
61	96	2010	53	Cefas G6	9/5/2010	n/a	n/a	29/5/2010	n/a	min 3	18; 15	n/a
62	87	2010	52	Cefas G6	10/5/2010	n/a	n/a	16/6/2010	n/a	min 2	15	n/a
63	76	2010	49	Cefas G6	10/5/2010	n/a	n/a	12/6/2010	n/a	min 2	16	n/a

Table S2. Percentage of turtle locations for (a) males, (b) females and (c) both males and females combined. A–C = main protection zones; "Buffer" = peripheral/buffer zone; "Outside"= outside the protected area boundaries; "Ecotourism" = currently suggested NMPZ ecotourism zone. Protected legislation is in place from May to October each year (grey area), with all other locations not receiving any protection.

(a) Males

Period	Turtles (n)	Locations (n)	Kernel analyses																	
			A			B			C			Buffer			Outside			Ecotourism		
			50	90	95	50	90	95	50	90	95	50	90	95	50	90	95	50	90	95
January	5	94	25.3	2.4	3.1	32.9	10.1	12.5	41.5	4.0	4.2	0	0	0	0.2	0.1	0.4	0	3.6	3.5
February	6	74	4.5	2.1	2.6	50.4	9.3	11.5	43.7	4.1	4.6	0	0.3	0.5	1.2	0.1	0.7	43.8	3.3	3.5
March	8	141	0	0.5	0.6	49.6	8.5	10.4	49.2	4.7	4.7	0	1.4	4.2	1.1	3.3	11.8	63.3	3.5	3.5
April	11	192	0	0.8	1.0	64.2	11.6	13.7	34.5	4.5	4.6	0	0.2	2.2	1.2	5.4	19.0	73.9	3.5	3.5
May	35	524	0	0.9	1.7	43.4	7.3	12.5	54.7	3.9	4.7	0	0.1	1.8	1.9	2.2	4.9	67.2	3.6	3.5
June	8	200	0	0.5	0.7	23.6	7.9	11.5	74.9	4.6	4.6	7.1	0.2	0.3	1.4	7.2	9.7	36.5	3.6	3.5
July	7	163	0	0.5	0.9	18.3	5.1	8.7	49.7	4.7	4.6	1.6	2.2	3.3	24.7	30.4	40.8	9.5	1.6	2.3
August	7	148	0	0	0	24.3	3.7	5.1	65.3	4.7	4.6	0	1.5	1.7	8.7	26.9	36.9	12.7	1.3	1.4
September	5	115	0	0.1	0.2	31.8	7.2	8.4	67.1	4.5	4.6	0	0.3	0.6	1.0	9.1	17.8	31.9	3.5	3.5
October	5	101	14.3	1.7	1.9	29.1	5.8	8.2	26.6	1.9	2.2	0	0	0	29.9	2.3	3.1	36.6	2.3	2.9
November	4	92	0	1.1	1.5	31.1	6.7	8.8	29.7	2.5	2.9	0	0	0	39.2	3.0	3.6	19.3	2.3	2.6
December		99	26.7	2.6	2.8	17.5	7.9	11.3	23.9	4.6	4.6	0	0.8	1.4	31.8	5.5	6.7	0	1.3	1.8

(b) Females

Period	Turtles (n)	Locations (n)	Kernel analyses																	
			A			B			C			Buffer			Outside			Ecotourism		
			50	90	95	50	90	95	50	90	95	50	90	95	50	90	95	50	90	95
May	23	298	8.8	4.3	4.8	68.5	11.3	15.9	30.5	4.2	4.5	0	0.2	1.6	0.9	0.5	8.4	64.1	3.2	3.5
June	28	306	17.1	4.8	4.8	59.0	11.1	15.4	31.2	3.3	4.3	0	1.2	2.4	0.9	0.9	4.5	46.3	3.5	3.5
July	18	109	25.1	4.8	4.8	59.6	15.1	16.7	22.6	4.6	4.7	0	4.9	8.1	0.6	13.4	26.6	75.0	3.5	3.5
August	1	8	0	0.9	1.0	74.3	4.5	5.7	0	0	0	0	0	0	0.3	0	0	63.7	2.2	2.5

(c) Males and females combined (only months where the two groups overlap are shown)

Period	Turtles (n)	Locations (n)	Kernel analyses																	
			A			B			C			Buffer			Outside			Ecotourism		
			50	90	95	50	90	95	50	90	95	50	90	95	50	90	95	50	90	95
May	58	822	0	2.8	4.5	51.7	9.5	14.5	46.7	4.1	4.6	0	0.1	2.3	1.5	1.8	6,7	73.3	3.5	3.5
June	36	506	0.4	4.6	4.8	48.8	11.5	16.5	49.5	4.4	4.6	0	0.9	1.9	1.1	5.4	9.1	57.7	3.5	3.5
July	25	272	0	4.9	4.9	39.7	14.6	17.7	43.2	4.6	4.6	4.8	4.2	6.3	12.1	27.5	44.0	24.6	3.5	3.5
August	8	156	0	0.5	0.7	24.8	7.1	9.9	58.6	4.6	4.6	2.5	1.5	1.7	14.1	28.1	37.0	11.8	2.8	3.2

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Chapter 7

Ontogeny of a new migration paradigm: Global Lagrangian analyses reveal that ocean currents drive sea turtle migration strategies

Rebecca Scott, Robert Marsh and Graeme C. Hays

Disclaimer: RS wrote this chapter and led/conducted all the analysis. GCH conceived the study, RM set up the ocean model so that RS could run the ocean model simulations.

Abstract

The factors that drive the diverse range of sea turtle migration strategies are poorly understood. Here, we test a hypothesis that the regular breeding migrations and foraging site selections of adult turtles are shaped indirectly by ocean currents based on the sites they experience whilst drifting as small hatchlings and imprinting. By analysing satellite tracking data from > 400 adult turtles (from 5 species and 42 nesting sites) in combination with c.45,000 Lagrangian hatchling drift scenarios (from surface drifter buoys and a state-of-the-art global ocean model) we provide support for this hypothesis on a global scale. Whilst adult turtles do not drift with ocean currents, their migrations are shaped by ocean current flows through two main mechanisms. Adults either (1) returned to foraging sites that they would have encountered whilst drifting as hatchlings (albeit, typically along a more direct route than the often convoluted routes of drifting hatchlings) or (2) foraged near to their natal area if the potential adult foraging sites that they drifted to as hatchlings were too far away to return on their regular to-and-fro breeding migrations. Consequently, unlike other long distance migrants, whose breeding migrations are shaped primarily through innate or socially learnt behaviours, the ontogeny of sea turtle migrations are driven by the ocean circulation system. Lagrangian analysis of ocean currents is thus anticipated to have great application for understanding of the migration strategies (1) of sea turtle populations under changing ocean circulation scenarios and (2) for populations that have yet to been tracked through satellite telemetry and (3) of other marine species with dispersal stages.

Introduction

Many animals are highly mobile, occupying different habitats at different life stages. For example, regular to-and-fro migrations between breeding and foraging habitats are a widespread phenomenon in the animal kingdom, and individuals often show high fidelity to both of their habitats (e.g. Broderick *et al.* 2007; Devlin *et al.* 2008; Baracho-neto *et al.* 2012), which in the case of Arctic terns (*Sterna paradisaea*) can be > 17,000 km apart (Egevang *et al.* 2010). Consequently, the biological and physical determinants of these movements, and the navigational cues and behaviours used to optimize travel between distant sites have received a lot of attention in recent years (e.g. Alexander 1998; Alerstem *et al.* 2003; Dingle and Drake 2007; Hein *et al.* 2012). For some species, migrations appear to evolve through social learning. For example, baleen whale calves that follow their mothers on their first migrations between tropical calving and high latitude feeding areas and later return independently to these same sites (Weinrich 1998). For other species, migrations appear to evolve through innate processes. For example, both the decision to migrate and the direction that an individual decides to migrate have been shown to be genetically pre-determined in some bird species (e.g. Berthold and Helbig 1992; Berthold and Terrill 1991).

A range of innate and learned behaviours have also been widely implicated in facilitating navigation between sites. When animals are within close proximity to previously encountered target habitats, organisms may use familiar sensory (olfactory, visual or audible cues etc) to aid navigation (Ueda *et al.* 1998; Otteson *et al.* 1990; Simpson *et al.* 2004). An innate ability to detect and use geomagnetic information from the Earth's magnetic field has also been widely implicated in the navigation of a range of organisms (Wiltschko and Wiltschko 2005). For example, laboratory experiments have revealed that neonate hatchling sea turtles can detect two components of the Earth's magnetic field; magnetic inclination and intensity (Lohmann *et al.* 2001; Putman *et al.* 2011). These two components are believed to provide turtles with a type of innate bi-coordinate magnetic map, from which both longitudinal and latitudinal information can be extracted (Putman *et al.* 2011). Indeed, this ability to use the Earth's magnetic field as a navigational sign post has been shown to help small hatchling sea turtles improve their survival chances whilst dispersing with ocean currents to their development habitats (Scott *et al.* 2012a; Putman *et al.* 2012a).

Satellite tracking technology has revolutionised our ability to study the migratory and navigational feats of large mobile organisms such as sea turtles (e.g. Block et al. 2011). Consequently, a wealth of data is now available detailing previously unknown ecological patterns in the post-breeding migrations of adult turtles from their natal beaches to their foraging areas (e.g. Godley *et al.* 2008). Synthesis of these datasets have highlighted four different migratory strategies for adult turtles (1) oceanic and/or coastal movements to fixed neritic foraging grounds (2) coastal shuttling between fixed or seasonal neritic sites (3) local residence and (4) pelagic foraging (Godley *et al.* 2008). Whilst adult hard shelled turtles (family Cheloniidae) tend to migrate to discrete neritic foraging grounds, migration strategies can vary widely between species, populations and individuals within a population. For example, post-breeding green turtles (*Chelonia mydas*) tracked from Ascension island all migrate c. 3000 km west along a narrow migratory corridor to foraging habitats off the coast of Brazil (Papi *et al.* 2000; Hays *et al.* 2002), whilst post-breeding green turtles from the Cocos (Keeling) forage (and remain resident) within this small island archipelago (Whiting *et al.* 2008). Some loggerhead turtles (*Caretta caretta*) from Cape Verde migrate c.1700 km SW to Sierra Leone, while others forage oceanically c.200-500 km east of the islands (Hawkes *et al.* 2006). Nonetheless, due to a tendency for adult cheloniid turtles to fast whilst away from their foraging habitats c. 3000 km appears to be the observed (and predicted physiological) upper limit on the one way post-breeding migration distance that an adult cheloniid turtle can travel (Hays and Scott in press).

Juvenile cheloniid turtles and adult leatherback turtles (*Dermochelys coriacea)*, the only species of soft shelled turtle (Dermochelyiidae family), can exploit foraging habitats much further (> 11,000 km) from their natal area as they feed en route (Witherington 2002; Boyle *et al.* 2009; Benson *et al.* 2011), and juveniles remain at their development sites for prolonged periods (years) before making a single return journey to back towards their natal area (e.g. Scott *et al.* 2012b). Thus, whilst satellite tracking studies have revealed that a range of post-breeding migration strategies are evident within this group, understanding the drivers that underpin the movement patterns and foraging habitat selections of adult turtles has remained enigmatic. Recent studies have thus highlighted the need for more quantitative and novel interdisciplinary approaches (e.g. Scott *et al.* 2012c; Hays *et al.* 2010).

Ocean currents influence the movements of all marine organisms due to the physical forces current flows exert on individuals and by shaping the distribution of food resources in the ocean (Lambardi *et al.* 2008). Indeed, due to their small size and weak swimming abilities, hatchling sea turtles are reliant on ocean currents to disperse to their development habitats. Whilst hatchlings are too small to be directly tracked at sea on these long journeys, global ocean circulation models and satellite tracked Lagrangian surface drifter buoys have recently gained great application for studying the dispersion of small organisms and life stages not amenable to direct tracking techniques (e.g. Hays and Marsh 1997; Hays *et al.* 2010; Shillinger *et al.* 2012; Scott *et al.* 2012ac; Putman *et al.* 2012ab). The movements of adult turtles are not directly shaped by current flows as they are powerful swimmers that can swim counter to strong opposing flows (Luschi *et al.* 2003). However, Lagrangian oceanography approaches have revealed that ocean currents may shape the migratory patterns and foraging site selections of adult sea turtles through an indirect mechanism; whereby adult turtles return to sites that they had previously encountered whilst passively drifting as small hatchlings (Hays *et al.* 2010).

This "hatchling drift hypothesis" was first proposed to explain the different migration strategies of loggerhead turtles tracked from their breeding grounds in Zakynthos (Hays *et al.* 2010). Broadly speaking, the north/south dichotomy in the post-breeding migrations and thus foraging sites of adult turtles was hypothesised to reflect the pattern of hatchling dispersion from this site due to a strong north/south dichotomy in the ocean circulation system near the breeding grounds. Thus, whilst the migrations of other species are driven by innate behaviours or social learning (e.g. Weinrich 1998; Berthold and Terrill 1991; Berthold and Helbig 1992), the work of Hays *et al.* (2010) alluded to a new paradigm that the ontogenetic development of sea turtles migrations may be driven by ocean currents. Here, by conducting a global meta-analysis of the post-breeding migrations of satellite tracked adult sea turtles and Lagrangian analysis of hatchling dispersion from these breeding grounds the new paradigm proposed by Hays *et al.* (2010) is tested on a global scale.

Methods

Adult satellite tracking data

A global meta-analysis of the post-breeding migrations of satellite tracked adult turtles was conducted. Both sexes were included in the analysis as the post-breeding

migrations of males are considered to be similar to female conspecifics (Godley *et al.* 2008). Six electronic literature databases were searched (Google Scholar, Scopus, ISI Web of Science, Science Direct, Seaturtle.org and the Marine Turtle Newsletter) using the following search terms: satellite tracking, sea turtle, marine turtle, breeding, foraging and migration along with the English and Latin names for each of the 7 turtle species. No restrictions on publication year were imposed. All sea turtle populations where ≥ 3 post-breeding individuals had been successfully tracked to their foraging locations were included in the analysis and longitude and latitude co-ordinates of the nesting and foraging locations of turtles were digitised from published maps. The published migration maps used in this study were all produced from Argos locations (operated by CLS Argos; http://www.argos-system.org) pre-filtered for accuracy using standard data filtering protocols (see for example, Blumenthal *et al.* 2006). Coordinates were plotted as global point shape files using the World Geodetic System (1984) in ESRI ArcGIS® (version 10) software.

Hard shelled turtles (Cheloniidae family) typically migrate to discrete neritic foraging grounds, defined here as habitats located on the continental shelf. Turtles were considered to have reached their foraging locations when the final locations of tracks showed a period of residence (typically weeks or months). However, some hard shelled turtles have been tracked to less discrete oceanic foraging areas. For example, loggerhead turtles tracked from the Cape Verde Islands spent several months to > 1 year foraging in oceanic habitats to the east of the Islands before tag transmissions ceased (Hawkes *et al.* 2006). Hence for these oceanic foragers, their final locations were used to represent the general vicinity of their foraging areas. Leatherback turtles (Dermochelyiidae family) do not migrate to discrete foraging sites; instead they continue to travel whilst foraging oceanically and can perform transoceanic wandering movements in the process (e.g. Fossette *et al.* 2010). Hence for leatherbacks turtles, we used all populations where ≥ 3 individuals were tracked for sufficiently long enough (typically > 1 year) to determine their general migration patterns. Since migratory end points could not be used to identify foraging grounds, we instead digitised the furthest location away from the breeding area to assess general migration patterns. In studies where individual leatherback tracks could not be identified in the spaghetti tracking plots of large numbers of turtles, we digitised locations of clearly defined high use

foraging areas; hotspots of prolonged foraging activity by one or multiple individuals (e.g. see Benson *et al.* 2011).

Lagrangian ocean current data: surface drifter buoys

Lagrangian drifter data were downloaded from the NOAA-AOML Global surface Drifter programme (http://www.aoml.noaa.gov/envids/). This dataset contains quality controlled data of > 14,500 satellite tracked surface buoys released since the 1970s. Buoys are deployed with drogues at 15m to reduce wind effects (i.e. a sub-surface sea anchor, a "drogue", is tethered to the surface buoy; Lumpkin and Pazos 2006). To capture potential hatchling drift scenarios, all buoys passing within 150 km of nesting sites where ≥ 3 post breeding turtles had been successfully tracked on their post-nesting migrations were selected, and upon first reaching this proximity, all subsequent fixes during the following ≤ 365 days of drift were used. No restrictions on date or drogue attachments were imposed. We looked at the first year of drift trajectories only, because as turtles develop their dispersal becomes less passive with increasing size and swimming strength.

Lagrangian ocean current data: ocean model simulations

In addition to using empirical Lagrangian drifter buoy data, 1000 1-year long passively drifting particle trajectories from the surface current fields of a state-of-the-art eddy-permitting ocean model hind cast were computed for each nesting site. The ocean model used in this study was developed at the National Oceanography Centre in Southampton based on a version of the NEMO model (the Nucleus for European Modelling of the Ocean; Madec 2008). Particle trajectories are tracked through an evolving model velocity field (Blanke *et al.* 2001) using the ARIANE program (http://stockage.univ-brest.fr/~grima/Ariane/). NEMO is forced with atmospheric conditions that combine 6-h air temperature, humidity, and wind fields from the ERA40 reanalysis with climatological radiation and freshwater fluxes from the CORE dataset (see Scott *et al.* 2012a). At eddy-permitting resolution, currents are realistically vigorous and ocean eddies are well resolved equatorward of mid latitudes. This leads to credible representation of both the mean advection and mesoscale spreading of passive drifters. Using ESRI ArcGIS 1000 randomly assigned particle release locations were generated between 10 and 60 km offshore from each nesting location to bracket estimates of the distance hatchlings are thought to travel during an initial week long swimming frenzy

period (Kraemer and Bennett 1981) and account for the different environmental conditions at each nesting site which might increase or decrease this distance. For each of the 1000 particle locations at each nesting location, a start year was assigned by selecting a year at random between 2000 and 2006. A start month and day was also assigned at random during the peak hatchling season (typically a 2-3 month window) at each site. Particle locations were computed at 5-day intervals and particles were constrained to remain at the uppermost NEMO depth level of 0.5 m as post-hatchlings reside at the surface and cannot dive deeply due to their positive buoyancy (Milsom 1975).

Testing the hatchling drift hypothesis

For most cheloniid turtle populations, turtles travel several 100s to 1000s of km through both coastal and oceanic waters to reach neritic foraging sites. For these populations, co-ordinates of the point where the movement paths of each buoy, particle and turtle first reached a straight line distance of 500km from the nesting site were used to calculate travel bearings. A distance of 500km was selected as (1) coastal processes often made it difficult to identify the initial (or general) travel direction of buoy/particle trajectories until they had established their course beyond the coastal realm and (2) 500 km captured the general travel directions of turtles that performed migrations of this magnitude, whilst ensuring a maximum number of buoys/particles were still drifting at this distance. Turtles that travelled along a bearing within 15° of a buoy or modelled particle trajectory bearing were considered to be travelling in the same direction as a Lagrangian hatchling drift trajectory, given the chaotic influence of mesoscale variability. For each population the proportion of observed turtle travel bearings that were within 15° of Lagrangian hatchling drift bearings were calculated. Randomly simulated turtle travel bearings were also generated (whilst taking into account land masses which precluded travel in certain directions) to assess the proportion of turtle bearings at each site that could be expected to travel within 15° of a Lagrangian drift trajectory by chance alone. By generating 1000 sets of random turtle bearings at each site, the number of random simulation sets where 0 bearings to n=the number of tracked turtle bearings were within 15° of drift bearings were calculated. Binomial tests were then performed for each population to assess if significantly more turtles were observed to travel along the same paths as ocean current flows than expected by chance.

For other turtle populations where all turtles were non-migratory (typically foraging a few 10's of km from there natal beaches), or all turtles performed coastal shuttling migrations (not crossing any open water), migration directions were not relevant/constrained to two directions along the coast. Hence, for these populations we qualitatively assessed if simulated particle trajectories and buoy trajectories could explain adult turtle movement patterns. For populations where all turtles foraged oceanically whilst performing pelagic wandering movements (e.g. all leatherback turtle populations), we looked at general migration patterns to see if broad scale population movement patters could be explained by Lagrangian drift scenarios.

Results

Adult satellite tracking data

Published satellite tracking data were obtained from 42 nesting sites where 3 to >100 turtles had been tracked on their post nesting migrations. Data were digitised for 243 cheloniid turtles; 78 loggerhead turtles (*Caretta caretta*), 26 green turtles (*Chelonia mydas*), 17 hawksbill turtles (*Eretmochelys imbricata*) and 21 olive ridley turtles *(Lepidochelys olivacea*). No data were available for two cheloniid species; the flatback turtle (*Natator depressus)* and Kemp's ridley turtle (*Lepidochelys kempii*). Data on the general movements of leatherback turtles were based on satellite tracking deployments on > 200 leatherback turtles (*Dermochelys coriacea*).

Lagrangian ocean current data: surface drifter buoys

A total of 1398 Lagrangian drifter buoys passed within 150 km of nesting sites, enabling 1794 1-year long Lagrangian hatchling drift trajectories to be derived (as some buoys passed the vicinity of ≥ 1 nesting sites; Fig. 1a). No buoy trajectories were available within 150 km from three nesting sites in Northern Australia and one nesting site on the Caribbean coast of Mexico. At five nesting sites there were > 100 buoys (Barbados, North Carolina, southeast Florida, American Samoa and Taiwan) and there were 50-100 buoys that drifted within the vicinity of a further 14 nesting sites. At other sites buoy data were more limited (< 50 buoys), and there were very limited buoy data available (< 10 buoys) for nesting sites in Zakynthos, south Gabon, Oman and Ecuador.

Lagrangian ocean current data: ocean model simulations

A total of 42,000 1-year-long Lagrangian trajectories were computed which produced > 3 million modelled particle locations (Fig. 1b). Whilst drifter buoys provided empirical observations of ocean currents to verify model simulations, ocean models enabled more detailed investigation into ocean currents experienced by hatchlings, with 1000 Lagrangian trajectories computed during the peak hatchling season at each of the 42 nesting sites. Model (*in silico*) Lagrangian trajectories and in-situ Lagrangian buoy trajectories revealed the same large-scale ocean circulation patterns (Fig. 1). However, the drift trajectories of buoys tended to travel further and captured a greater spread of drift scenarios than model simulations. This is to be expected, as model simulations will not resolve some of the smaller scale ocean circulation features (e.g. small eddies) that will influence the trajectories of surface drifters. From hereafter the term "Lagrangian drifter/trajectory" is used to refer to both surface drifter buoy and modelled particle trajectories as the number of modelled trajectories tended to dominate over buoy trajectories by more than 10:1 at the majority (88%) of the nesting sites.

Support for the hatchling drift hypothesis

The post breeding migrations of all adult cheloniid turtle populations could be explained by Lagrangian hatchling drift trajectories through two main mechanisms (Fig. 2). Firstly, adults returned to sites they would have encountered as hatchlings (albeit typically along a more direct route than the often convoluted routes of drifting hatchlings). Secondly, the nearest potential adult foraging sites that hatchlings drifted to were too far away from their natal area to return as adults on their regular breeding migrations, hence adult turtles remained locally resident at their natal area or foraged oceanically (if an island rookery), or performed coastal/shuttling migrations to fixed/seasonal habitats (if a mainland rookery). Due to the different foraging strategy of leatherback turtles their migrations are discussed separately.

Support for the first mechanism: Case 1

Support for this first mechanism was strongest for 5 populations where ocean currents flows showed strong directionality (Fig. 3; Figs. S1a;b). For example, at Ascension Island all Lagrangian drifters travelled broadly west towards the coast of Brazil. All of the 20 green turtles tracked from this site also migrated c. 3000 km west towards foraging habitats along the coast of Brazil (Papi *et al.* 2000; Hays *et al.* 2002; Fig. 3a).

At other sites, there was a marked divergence in the directions travelled by Lagrangian drift trajectories. For example, offshore from the Guangdong province in China, drifters travelled broadly NE or SW with a bifurcation in ocean current flows and offshore from the Greek island of Zakynthos, drifters travelled broadly NW, SW or SE with a trifurcation in ocean current flows. From China, all green turtles migrated broadly NE or SW (Song *et al.* 2002; Chan *et al.* 2003; Fig. 3b). From Zakynthos, all turtles that left Greek waters travelled broadly NW, SW or SE (Zbinden *et al.* 2007; Schofield *et al.* 2009; Hays *et al.* 2010; Fig. 3c.). At these three sites and two other sites, Taiwian (Cheng 2000; Fig. S1a) and Puerto Rica (Van Dam *et al.* 2008; Fig. S1b), significantly more turtles than expected by chance migrated in the same direction as ocean current flows ($P < 0.002$ in all cases; Fig. 3, Figs. S1a,b). Furthermore, no turtles migrated along routes that differed to passive routes taken by Lagrangian drifters, hence these populations provide compelling support for the hatchling drift hypothesis.

Support for the first mechanism: Case 2

Turtles tracked from a further 19 nesting sites also provided support for the first hypothesis. However, at these sites ocean currents flows tended to be more dispersed and turtles migrated along a subset of a wide range of routes they could have encountered, or turtles travelled along different (more direct routes) to habitats they would have encountered as hatchlings (along more indirect dispersal routes). Hence at these sites, due to the wide spread in drifter trajectories, turtle migration routes were not significantly correlated with drift routes (more than to be expected by chance) or turtles migrated along entirely different routes to drifters. For example, all drifters from Tortuguero national park (on the Caribbean coast of Costa Rica) initially drifted east along the coast of Panama towards Columbia in a large eddy before looping back broadly NW towards Nicaragua, Honduras, Belize and Mexico. All 10 green and 2 hawksbill turtles tracked from this site migrated broadly NW along more direct routes, and opposing the initial easterly flowing currents, to foraging grounds in Nicaragua, Honduras and Belize (Fig. 4a; Troëng et al. 2005a;b). All 20 green and 12 olive ridley turtles tracked from three different nesting sites in Northern Australia (Whiting *et al.* 2007; Kennet *et al.* 2004; McMahon *et al.* 2007) migrated to foraging habitats along a subset of a broad range of drift trajectories (Fig. 4b; Fig. S2a;b). At the Ogasawara Islands (c. 1000 km south of mainland Japan) local retention was high for some drifters due to strong eddy variability whilst other drifters started to head along trajectories that

would lead to transoceanic movements in the North Pacific Gyre. Here turtles migrated c.1000 km NNW to mainland Japan; the nearest land mass from their natal rookeries that they would have encountered before embarking on any transoceanic journeys (Fig. 4c; Hatase *et al.* 2006). From the Eastern Atlantic Cape Verde islands, the currents flow broadly west in North Atlantic Gyre. However three turtles tracked from this site migrated along south easterly trajectories to foraging sites along the coast off Sierra Leone (Fig. 4d; Hawkes *et al.* 2006). Some of the Lagrangian drift trajectories that initially drifted west, left the North Atlantic gyre, and then also drifted south east to the coast of Sierra Leone. Hence we propose that these turtles also followed this convoluted drift trajectory to Sierra Leone as hatchlings, but then returned directly as adults. Thus, whilst support for the hypothesis from case 2 populations was not as compelling as the support from case 1 populations, these populations provide further evidence as no turtles sites migrated to foraging habitats that they could never have encountered as drifting hatchlings (see supplementary Figs. S2a-m for further case 2 populations).

Support for the second mechanism: Case 3

There were 7 nesting sites where the nearest land mass (and thus potential adult cheloniid neritic foraging grounds) "downstream" of prevailing ocean current flows was too far (> 3000km; Hays and Scott in press) for an adult cheloniid turtle to travel on a regular post-breeding migration. For example, from the eastern Indian Ocean Cocos (Keeling) Islands Lagrangian drifters travelled broadly south or west with the Indian Ocean Gyre and the nearest land mass encountered (Madagascar/East Africa) was > 5000 km away (Fig. 4e). A similar scenario occurred at mainland sites (e.g. in the southeastern USA) where drifters were transported > 5000 km with the North Atlantic gyre to Eastern Atlantic habitats (Fig. 4f).

At island sites, where downstream land masses were too far for regular cheloniid post-breeding migrations, adult turtles remained locally resident within the archipelago; for example green turtles from the Cocos (Keeling) Islands (Whiting *et al.* 2008; Fig. 4e) or hawksbill turtles from the Seychelles (Mortimer and Balazs 2000; Fig. S3a). From the Cape Verde islands, most post-nesting loggerhead turtles foraged oceanically; an untypical strategy for a hard-shelled turtle. Unlike the aforementioned three turtles from Cape Verde that migrated southeast to neritic habitats, these turtles (like the majority of Lagrangian drifters) are predicted to have remained on transoceanic hatchling drift

trajectories in the North Atlantic gyre. These hatchlings would not have encountered any land masses until crossing the Atlantic Ocean and reaching the Caribbean (> 4000km away) or the Bahamas (> 6000km away). Hence, we propose that their oceanic foraging habitats are likely to reflect the fact that neritic foraging habitats around the Cape Verde Islands are limited and they are unaware of any other suitable (and more productive) neritic habitats nearby. Indeed, other recent studies have also alluded to the same explanation as to why these Cape Verde turtles and other adult cheloniid turtles would forage in suboptimal oceanic habitats (Eder *et al.* 2012).

At mainland nesting sites where downstream land masses were too far, turtles may travel further distances but consistently travelled along the coast from their natal area to fixed or seasonal neritic habitats. For example, this was the case for loggerhead turtles from North Carolina (Hawkes *et al.* 2007; Fig. 4f) and south east Florida (Ardent *et al.* 2012; Fig. S3b). At these sites, foraging habitats selections are expected to occur based on the habitats encountered as larger juveniles/sub-adults that recruit back to coastal development habitats and any exploratory movements along the coast/offshore from their natal area by adults. Any directional movements may thus not reflect current flows experienced as small hatchlings. For example, ocean circulation off the coast of South Africa is governed by the southerly flowing Angulhas current. Whilst the southerly movements of leatherback turtles tracked from this region are in accordance with the broad scale dispersion of drifters from this region (Fig. 4g; see also Lambardi *et al.* 2008), three loggerhead turtles also tracked from this site migrated c. 500km North (Luschi *et al.* 2006), opposing the strong southerly flows that would have transported hatchlings south, then east or west to very distant land masses. The fact that cheloniid turtles adopted one of the less typical migratory strategies (local residence, coastal shuttling or oceanic foraging) at all of the nesting sites where the locations of potential neritic foraging habitats downstream of current follows exceeded the upper limit on their migration distances provides further compelling support for the drift hypothesis. Furthermore, distances of the nearest landmass land masses (and thus potential adult cheloniid neritic foraging grounds) "downstream" of prevailing ocean current flows were significantly further at these sites (mean =5781 km; SD=1525 km) than other cheloniid nesting sites than other cheloniid nesting sites (mean= 600 km; SD= 555 km) where turtles migrations supported the first mechanism of the hypothesis ($W= 351.00$; $P < 0.001$; see supplementary Figs. S3a-c for further case 3 populations).

Leatherback turtles: Case 4

Leatherback turtles wander the oceans exploiting patchily distributed pelagic prey resources (Fosette *et al.* 2010). Their post-breeding movements are thus influenced by ocean currents more directly than other cheloniid turtles; as oceanographic features such as mesoscale eddies, convergences and upwellings concentrate the macroplankton on which they feed (e.g. Lambardi *et al.* 2008). Indeed, our analyses shows that their broad scale movement patterns are in accordance with the broad scale patterns in the global ocean circulation (Fig 4g; Figs. S4a-d). More detailed analysis into the tracks of the aforementioned leatherback turtles from South Africa (Fig. 4g) by Lambardi *et al.* (2008) revealed that the movements of these turtles were virtually indistinguishable from those of Lagrangian drifters. Consequently, since it is now well established that leatherback drift/wander through the oceans exploiting new food patches and hence do not travel to target destinations like cheloniid turtles (e.g. Lambardi et al. 2008; Fosette et al 2010), further discussion of our findings focuses on the novel and indirect paradigm through which ocean currents drive the ontogeny of cheloniid turtle migrations.

Discussion

By conducting a global meta-analysis of the post-breeding migrations of adult turtles coupled with Lagrangian oceanography analysis of the passive dispersion of hatchling turtles, we provide compelling evidence that ocean currents drive the ontogeny of sea turtle migration strategies. The hatchling dispersal phase is the least understood sea turtle life history stage and knowledge of the location and duration of this phase is scarce/non-existent for most sea turtle populations (e.g. see Bolten 2003). By conducting the first global Lagrangian analysis of hatchling dispersal, we thus provide key information on global dispersion patterns of hatchlings and highlight that the importance of studying hatchling dispersal extends beyond the direct implications for the early life history stages, to implications for turtles throughout adulthood.

By extending the new migration paradigm proposed by Hays *et al.* (2010) to a global scale, we reveal two mechanisms through which ocean currents drive the migrations and foraging site selections of adult turtles. For most populations, the movements of adult turtles could be explained through the first mechanism; whereby adult turtles return to sites that they would have encountered as drifting hatchlings. Support for this first

mechanism was strongest at nesting sites like Ascension Island, Zakynthos and China where ocean current flows and sea turtles show strong directionality and overlap in their movement pathways. For example, the orientations of both ocean currents and green sea turtle migratory routes are broadly zonal, between Ascension Island and Brazil. However, suitable habitats where other green turtle populations are known to forage also exist at closer/similar distances to the north and east of Ascension Island (e.g. in Guinea Bissau; Godley *et al.* 2010 and Gabon: Sounguet *et al.* 1994). As we predict, no Ascension turtles will migrate to these sites if they have never drifted there. At the majority of nesting sites ocean current flows were more dispersed, however there was still strong support for the hypothesis as adult turtles consistently migrated to sites that they would have encountered as hatchlings.

Whilst hatchlings may drift to many different sites during the dispersal phase, adult turtles can use their past experiences as hatchlings to return to the most suitable adult foraging habitats. Due to the high mortality rates of hatchlings during the juvenile dispersal phase, one would expect a strong selective pressure for turtles that survive to maturity to imprint on (and return to) successful foraging sites that they had encountered. This hypothesis is further supported by the fact that sea turtles are already known to be able imprint on their habitats, because adult turtles show high philopatry to their natal areas and fidelity to their foraging habitats (Broderick *et al.* 2006; Lee *et al.*2007). Indeed, other marine species with juvenile dispersal phases, also imprint on natal sites as juveniles and later return as adults (e.g. Quin and Dittman 1992) and it has been suggested that both fish and sea turtles can use the Earth's magnetic field to return to these sites (Lohmann *et al.* 2008).

Further support that ocean currents drive the ontogeny of sea turtle migrations is proposed through a second mechanism; where-bye the potential adult foraging habitats that hatchlings encounter whilst drifting are simply too far away for adult turtles to return on their regular post-breeding migrations. The distance of land masses "downstream" (with ocean current flows) from nesting rookeries, thus also drives the ontogeny of cheloniid turtle migrations. Indeed, for sites where the nearest land masses hatchlings drifted to with prevailing current flows were > c.4000 km away from the natal area, adult cheloniid turtles adopted one of the less typical migratory strategies. For example, at various island archipelago nesting sites turtles remained locally resident

within the archipelago (Mortimer and Balazs 2000; Whiting *et al.* 2008) or foraged relatively nearby in oceanic waters (Hawkes *et al.* 2006). At mainland sites, turtles performed entirely coastal migrations to fixed or seasonal habitats (Luschi *et al.* 2006; Hawkes *et al.* 2007; Ardent *et al.* 2012). Hence at these sites, the movements and foraging habits of adult turtles are proposed to be driven by more recent habitats that they encounter during their return trips to their natal area and other exploratory movements around the natal area.

Whilst it is well established that hatchlings are reliant on ocean currents to reach their development habitats (e.g. Bolten 2003), there is growing evidence from loggerhead turtle populations in the North Atlantic that they can also embark on periods of active swimming which may alter their dispersal trajectories (Scott *et al.* 2012a; Putman *et al.* 2012a;b). If hatchlings from the SE USA are advected by the North Atlantic current, which branches off from the northern boundary of the warm North Atlantic Gyre circulatory system and flows towards the cold waters of Northern Europe they will die from cold stunning (Witt *et al.* 2007; Monzón-Argüello *et al.* 2012). Laboratory experiments where hatchlings were exposed to geomagnetic signatures of the Earth's magnetic field at the northern boundary of the gyre, revealed active swimming broadly directed towards the centre of the gyre. Later studies revealed that small bursts of directional swimming using the Earth's magnetic field as a navigational sign post, can help small hatchlings to stay on favourable southerly drift trajectories within the Gyre thus greatly improving their survival chances (Scott *et al.* 2012a; Putman *et al.* 2012a;b). Nonetheless, hatchlings exposed to geomagnetic signatures of the Earth's magnetic field at safer southerly latitudes within the gyre, do not show any directional swimming in response to the Earth's magnetic field (e.g. Lohmann *et al.* 2001). Hence for turtles drifting along safe trajectories there is no evidence for any innate behaviour that may alter their general dispersal pathways. Since the focus of our findings, were on surviving hatchlings that drifted to favourable sites, where they later returned as adults, the influence of any active swimming behaviour on our findings is likely to minimal. Nonetheless, due to the high mortality rates of hatchlings, particularly those in unfavourable current flows, adult migrations will only reflect a subset of the "successful" Lagrangian drift trajectories.

The assumptions that the passive dispersion of hatchling sea turtles will reflect the passive dispersion of in situ and simulated floating drifters have been discussed in detail previously (e.g. Hays *et al.* 2010; Scott *et al.* 2012b). Indeed, studies where populations specific genetic markers are used to assign juvenile turtles captured at their foraging grounds to their natal rookery of origin have revealed that juvenile foraging sites are predictably located downstream of prevailing ocean currents (e.g. Bolten *et al.* 1998; Boyle *et al.* 2009; Blumenthal et al 2009; Monzón-Argüello *et al.* 2010) Nonetheless, extreme weather events like large storms can displace hatchling sea turtles 1000s of km along aberrant dispersal routes not captured by surface drifter buoy data or model simulations (e.g. Monzón-Argüello *et al.* 2012). Consequently, with increased storm activity predicted under future climate change scenarios (Webster *et al.* 2005), if hatchlings survive displacements and arrive at favourable habitats, storms may play an increasing role in shaping the ontogeny of sea turtle migrations. Particularly since the behavioural plasticity of sea turtle migrations can help ensure a greater ability to adapt to changing conditions.

By analysing 7 years of global surface current flows from 42,000 *in silico* Lagrangian drift trajectories supplemented by 1794 surface drifter buoy trajectories (spanning the years 1981-2011), our global analysis would have captured aspects of both intra-annual and inter-annual variability in prevailing ocean circulation patterns; the primary determinant of hatchling dispersal and adult migrations. Reassuringly, our global analysis revealed the same broad scale ocean circulation patterns as other site specific studies where higher resolution regional models and/or more detailed analysis into intra/inter-annual variation in ocean currents have been carried out (e.g. Hays *et al.* 2010; Gasper *et al.* 2012; Putman *et al.* 2012b). By testing the hatchling drift paradigm proposed by Hays *et al.* (2010) on a global scale, significant advances have been made with regards to understanding the drivers that underpin the diverse range of sea turtle migrations strategies and foraging habitats.

Large marine vertebrates face particularly high risks from anthropogenic activities in their foraging habitats (Hooker and Gerber, 2004) and the foraging habitats of sea turtles have been identified as important marine ecosystems worthy of protection (Scott *et al.* 2012c). Understanding the biological and physical determinants of their migrations and foraging habitat selections is thus key for effective conservation

management strategies such as the designation of Marine Protected Areas. Consequently, it is hoped that the potential for Lagrangian oceanography approaches to aid understanding into the migrations of other marine species with dispersal life stages, and for other sea turtles populations without established satellite tracking projects is highlighted, and that with emerging datasets our hypothesis will be further supported, tested and refined.

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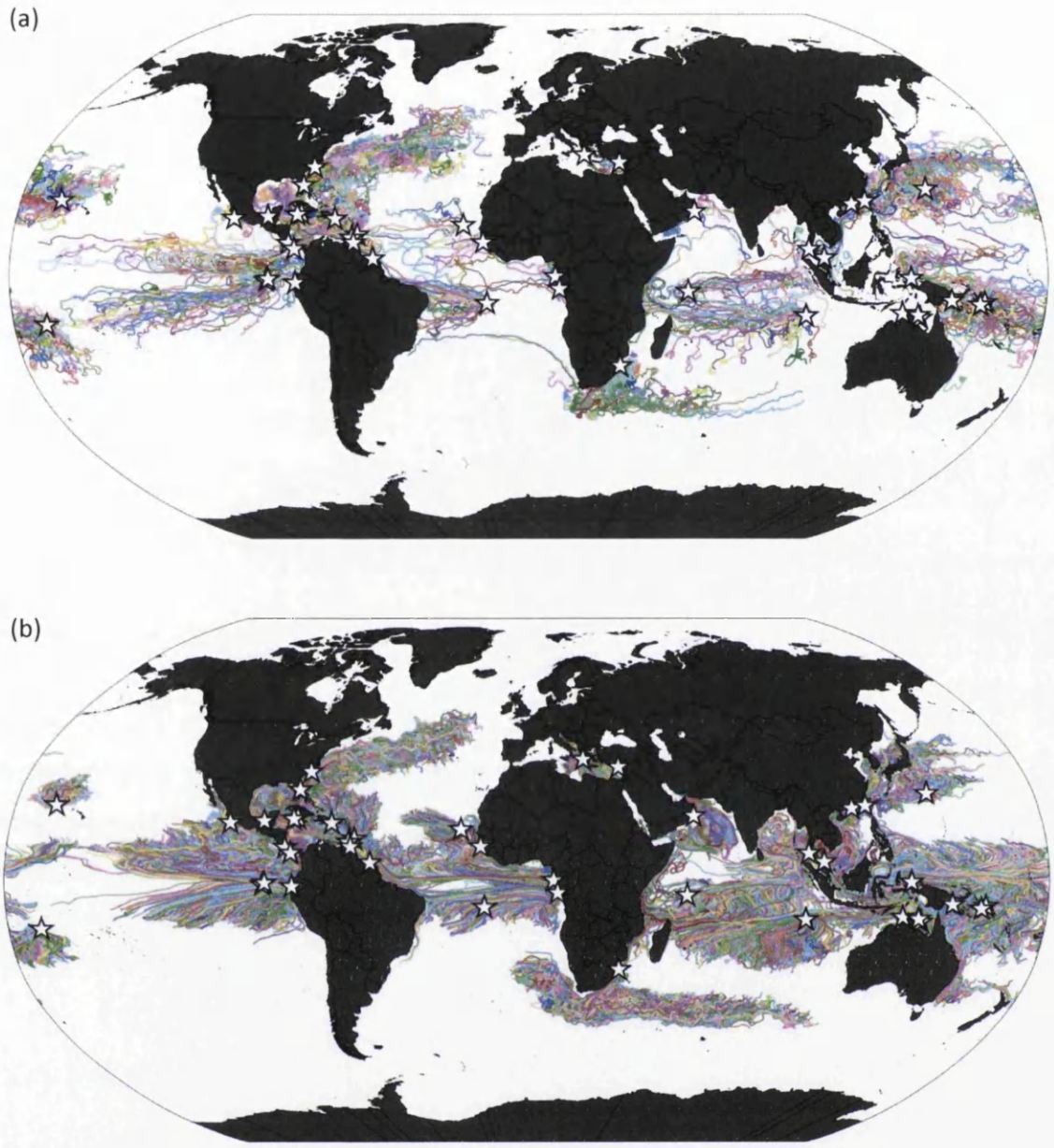

Fig. 1 Lagrangian hatchling drift trajectories for 42 nesting sites (denoted as stars). (a) 1794 1-year long trajectories derived from 1398 surface drifter buoys (spanning the years 1981-2011). (b) 42,000 1-year long particle trajectories derived from NEMO simulations (during periods of peak hatchling emergence, spanning the years 2000-2006). The large-scale circulation is broadly similar in both observed and simulated drifts: within ±15° of the Equator, flows are predominantly westward, incorporating some Ekman divergence about the Equator itself; in the subtropics, drifts follow the major western boundary currents, most conspicuously the Gulf Stream, the Kuroshio, the Agulhas, and the East Australian Currents; elsewhere in the subtropics, flows are sluggish and less organized.

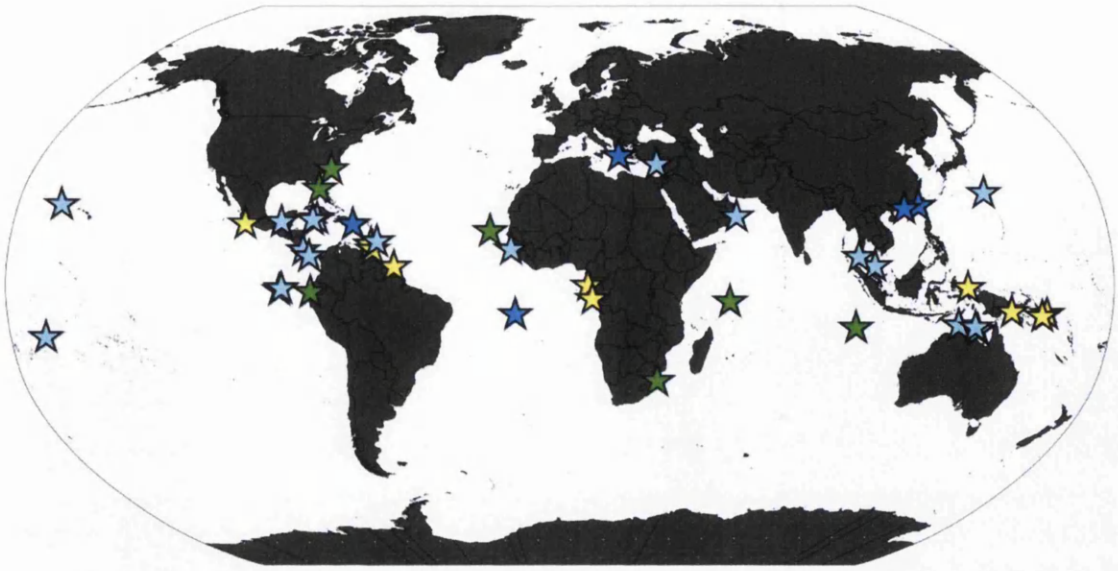

Fig. 2. Global support for the hatchling drift hypothesis. Dark blue stars: cheloniid nesting sites where there was a strong directionality in prevailing ocean currents flows and a significant overlap in the directionality of adult turtle migrations. Light blue stars: cheloniid nesting sites where ocean current flows were more dispersed and adult turtles migrated to a subset of foraging sites they would have encountered as drifting hatchlings. Green stars: cheloniid nesting sites where prevailing ocean currents transported hatchlings to foraging sites that were too far from the natal area to return as adults. Yellow stars: Dermochelyiidae nesting sites where leatherback turtles were tracked on their pelagic foraging movements. Leatherback turtles were also tracked from South Africa (coded with a green star; see Fig. 4g.).

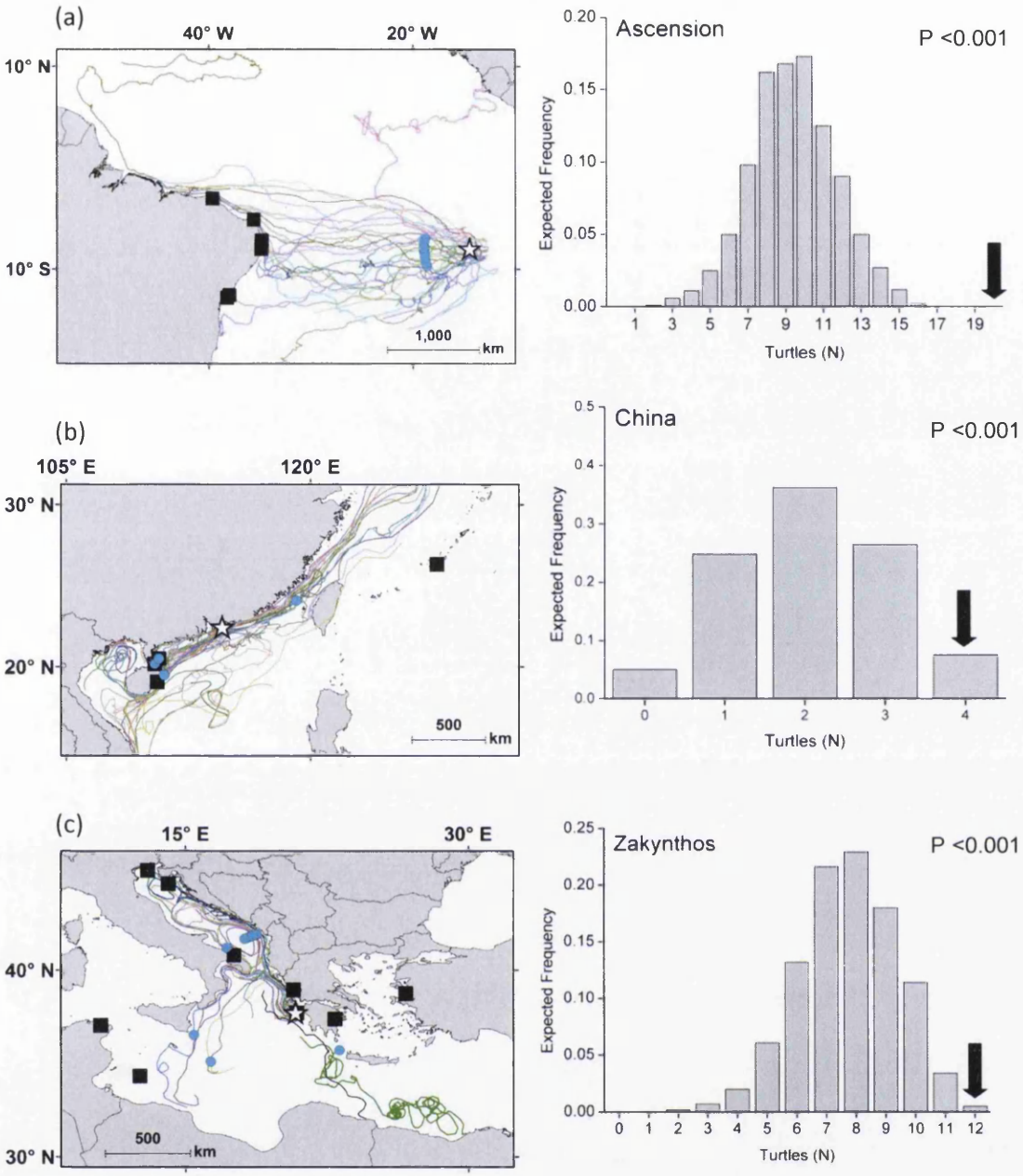

Fig. 3. Support for the first mechanism of the drift hypothesis, case 1. populations: (a) Green turtles (n=20) tracked from Ascension Island (Papi *et al.* 2000; Hays *et al.* 2002). All turtles migrated west towards the coast of Brazil, eight of which reached their final foraging locations in Brazil. All Lagrangian drifters also travelled broadly west towards the coast of Brazil, however it is noteworthy that two drifters (both buoys) then started to head broadly NE (b). Green turtles (n=4) tracked from China (Song *et al.* 2002; Chan *et al.* 2003). Three turtles migrated WSW to south China, while one turtle migrated NE to Okinawa island, Japan. 76 % of Lagrangian drifters from this site travelled WSW while 14 % of drifters travelled NE. (c) Loggerhead turtles (n=17) tracked from Zakynthos (Zbinden *et al.* 2007; Schofield *et al.* 2009; Hays *et al.* 2010). Ten turtles migrated north to foraging locations in the Adriatic, two migrated

SW to Libya and Tunisia, one migrated broadly SE then east to Turkey, four remained in Greek waters. The majority (> 90%) of Lagrangrian drifters travelled north into the Adriatic, the other drifters travelled broadly SW or SE. Left panel symbols: coloured lines represent a selection of (c. 25-50) drift trajectories to reflect the spread in drift scenarios at each nesting site (star); blue circles correspond to turtle locations 500 km from their natal area (used to derive travel bearings), black squares correspond to turtle foraging locations. Right panel symbols: black arrows correspond to the number of turtles observed to travel within 15° of Lagrangian drifter bearings, histogram bars refer to the proportion of 1000 simulations where 0 to n=the number of randomly generated tracked turtle bearings were within 15° of Lagrangian drifter bearings. For all populations significantly more turtles travelled in the same direction as Lagrangian drifters than could be expected by chance alone (P values, right panels).

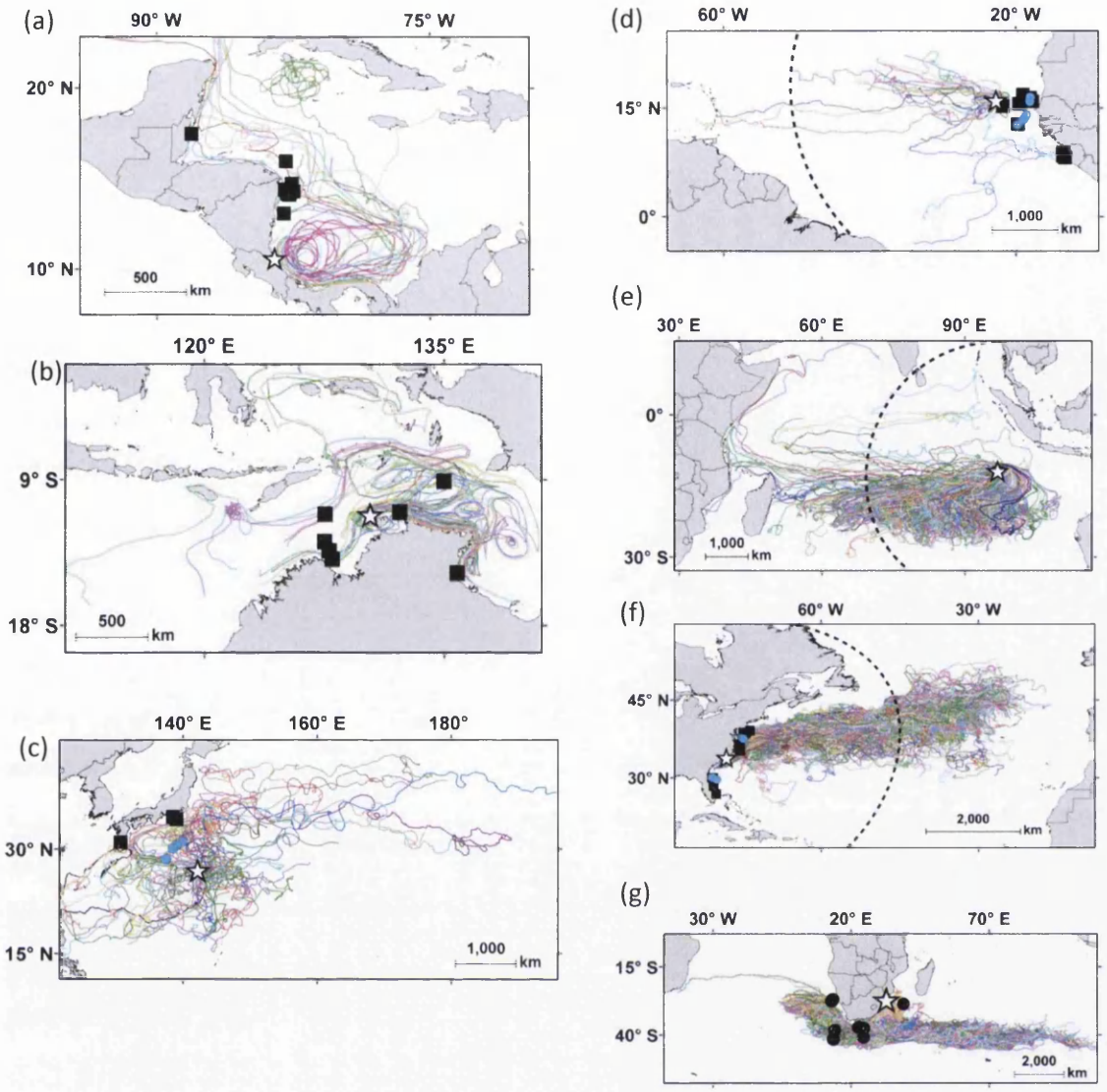

Fig. 4. Support for the first (case 2 populations: a-d) and second mechanisms (case 3 populations: d-g) of the drift hypothesis. (a) Green (n=10) and hawksbill (n=2) turtles tracked from Tortuguero, Costa Rica (Troëng *et al.* 2005a;b). All drifters were initially entrained in an area of high eddy activity, but broadly speaking tended to drift east towards Panama and Columbia before looping back and drifting NW towards Nicaragua, Honduras and Belize. All turtles migrated along more direct routes broadly NW to Nicaragua, Honduras and Belize (b) Olive Ridley turtles (n=8) tracked from the Tiwi Islands, North Australia (Whiting *et al.* 2007). All turtles migrated along a subset of a range of potential Lagrangian drift routes to their foraging habitats (c) Green turtles (n=4) from the Ogasawara Islands (Hatase *et al.* 2006). The majority of drifters were initially retained in eddies which spread from the natal area in all directions before starting to drift along transoceanic journeys in the North Pacific gyre. The nearest land mass drifters encountered before drifting broadly east in the Gyre was mainland Japan. All turtles travelled directly NNW

c. 1000 km towards mainland Japan, three of which reached their foraging grounds there (Hatase *et al.* 2006). (d) Loggerhead turtles (n=10) from the Cape Verde Islands (Hawkes *et al.* 2006). Seven turtles foraged in oceanic waters. All drifters started to embark on westerly trajectories in the North Atlantic gyre where they would not encounter land mass for > 4000 km along this trajectory. Three turtles migrated SE to the coast of Sierra Leone; the only land mass encountered by drifters within 3000 km (dashed line) of the natal area. However, these drifters reached Sierra Leone along more convoluted routes, initially travelling west and then SE. (e) Non-migratory green turtles (n=6) from the Cocos (Keeling) Islands (Whiting *et al.* 2008). Drifters travelled broadly west and south and did not encounter land mass until crossing the Indian Ocean and reaching the coasts of Madagascar and East Africa (> 5000 km away). Only two drifters passed close to other land masses within a 3000 km buffer of the natal area (dashed line) drifting near Indonesia and into the Bay of Bengal. (f) Coastal shuttling loggerhead turtles (n=12) from North Carolina (Hawkes *et al.* 2007) Turtles travelled north or south along the coast to fixed/seasonal coastal habitats. (g) Leatherback (n=9) and loggerhead (n=3) turtles from South Africa (Luschi *et al.* 2006). The foraging movements of leatherback turtles were in close association with southerly flowing Angulhas current and areas of high eddy activity. Three loggerhead turtles all migrated north along the coast. Drifters entered both the Indian and South Atlantic Oceans, transporting hatchlings too far away from their natal area to return as adults. Map symbols follow those detailed in Fig. 3 for panels a-d and for panels e-g all drifter trajectories (> 1000 at each site) are plotted. Turtle locations at 500 km (blue circles) are only plotted for populations where $\geq$ 3 turtles performed migrations of this magnitude.

Appendix 7

Support for the first mechanism of the hatchling drift hypothesis: Case 1 populations

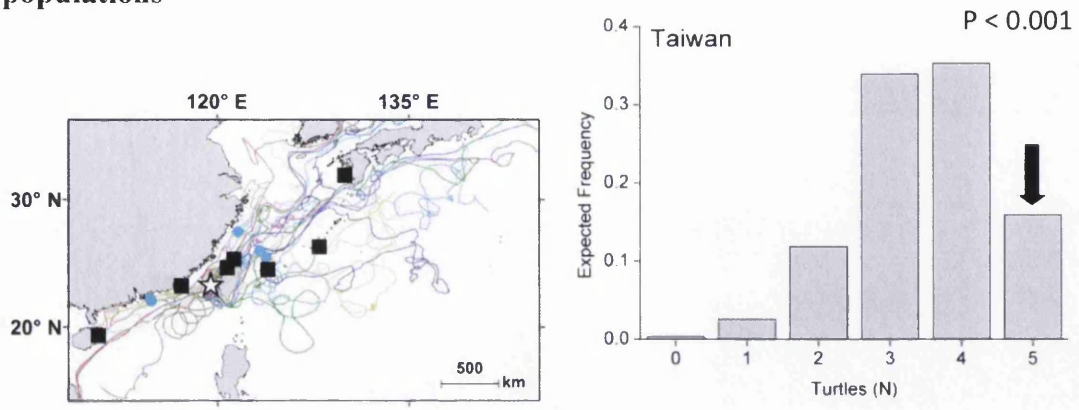

Fig. S1a. Green turtles (n=8) from Taiwan (Cheng 2000). Turtles migrated along broadly NE or SW trajectories in accordance with the bifurcation of drifters, seven of which reached their foraging habitats. Left panel symbols: coloured lines represent a selection of (c. 25-50) drift trajectories to reflect the spread of drift scenarios from the natal area (star), blue circles correspond to turtle locations at 500km (used to derive travel bearings), black squares correspond to turtle foraging locations. Right panel symbols: black arrows correspond to the number of turtles observed to travel within 15° of Lagrangian drifter bearings, histogram bars refer to the proportion of 1000 simulations where 0 to n=the number of randomly generated tracked turtle bearings were within 15° of Lagrangian drifter bearings. Significantly more turtles travelled in the same direction as Lagrangian drifters than could be expected by chance alone (P values, right panels).

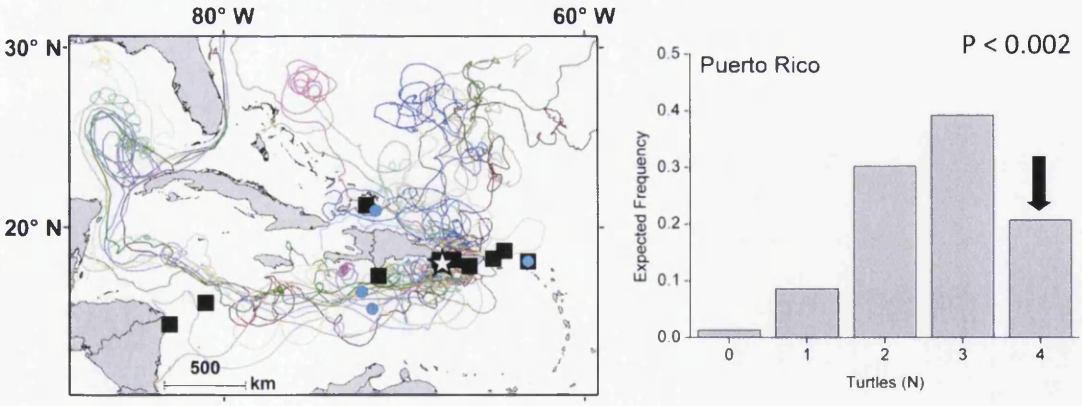

Fig. S1b. Hawksbill turtles (n=15) tracked from Mona Island, Puerto Rica (Van Dam *et al.* 2008). Eight turtles foraged locally around Puerto Rica, three turtles migrated east towards the US and British Virgin Islands and the French west Indies. One turtle migrated NW towards the Turks and Cacos Islands, three turtles migrated broadly west to Dominica Republic, Nicaragua

and Honduras. c. 60 % of Lagrangian drifters travelled broadly north or east of the Dominican Republic, the rest travelled broadly west along the southern coast of the Dominican Republic, into the Caribbean Sea and towards the coasts of Nicaragua, Honduras, Belize and Mexico. c. 32% of drifters entered the Gulf of Mexico and 28% drifted east of Florida in the Gulf Stream. Significantly more turtles than could be expected by chance migrated in the same direction as drifters. Panel symbols follow those detailed in Fig. S1a.

Support for the first mechanism of the hatchling drift hypothesis: case 2 populations

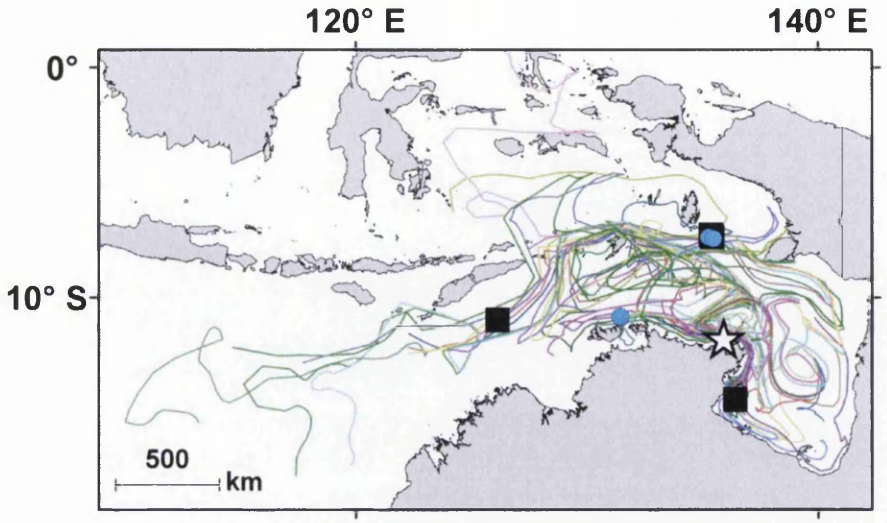

Fig. S2a. Olive ridley turtles (n=4) from the Wessel Islands (McMahon *et al.* 2007). All turtles migrated along a subset of a range of drift trajectories. Buoys dispersed widely, with c.50% first entering the Gulf of Carpenteria (where one turtle migrated), before remaining in the Gulf of Carpenteria or streaming broadly north then west. Coloured lines represent a selection of (c. 25-50) drift trajectories from the natal area (star) to reflect the range of drift scenarios, blue circles correspond to turtle locations at 500km (displayed only for populations where ≥ 3 turtles travelled > 500km), black squares correspond to turtle foraging locations.

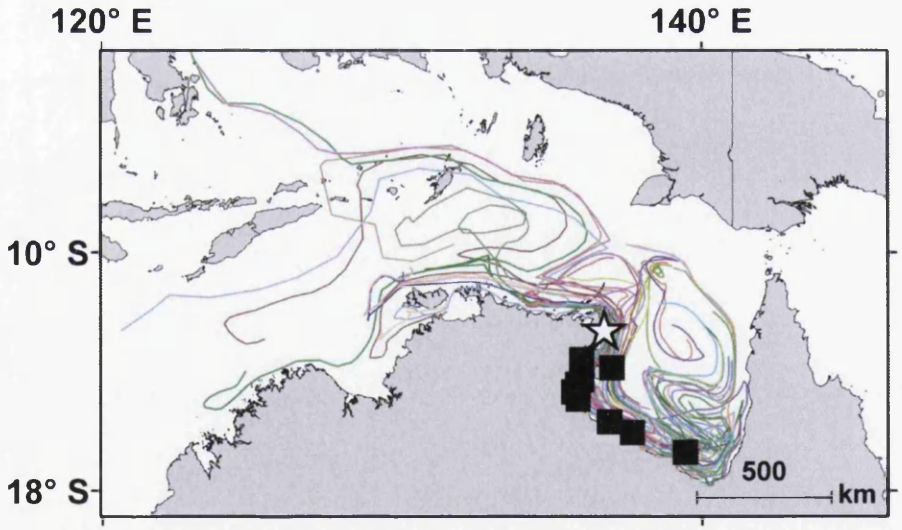

Fig. S2b. Green turtles (n=20) tracked from Djulpan nesting beach (Kennet *et al.* 2004). All turtles migrated into the Gulf of Carpenteria. The majority (> 99%) of buoys also drifted into the Gulf of Carpenteria, 36% of which then left the Gulf and drifted broadly west. Symbols follow those detailed in Fig. S2a.

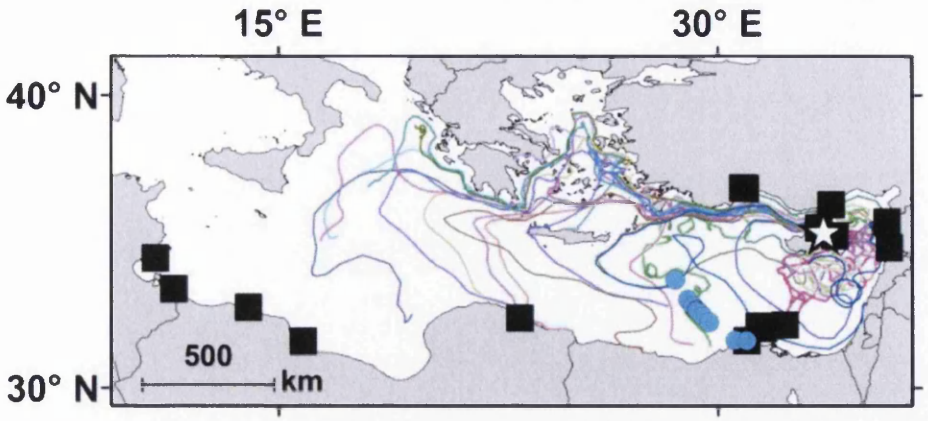

Fig. S2c. Green (n=10) and loggerhead (n=10) turtles tracked from Cyprus (Broderick *et al.* 2007; Godley *et al.* 2002; Godley *et al.* 2003). All Lagrangian drifters that travelled > 500 km drifted north to the coast of Turkey and then west before looping back round to various sites along the south and east boundaries of the eastern Mediterranean basin. Turtles that travelled > 500km however took more direct routes (along SW trajectories) to sites in the southern basin that they would have passively drifted to. Individuals that travelled shorter distances all foraged around the coast of Turkey, Cyprus and Syria; again to sites they would have encountered whilst drifting. Symbols follow those detailed in Fig. S2a.

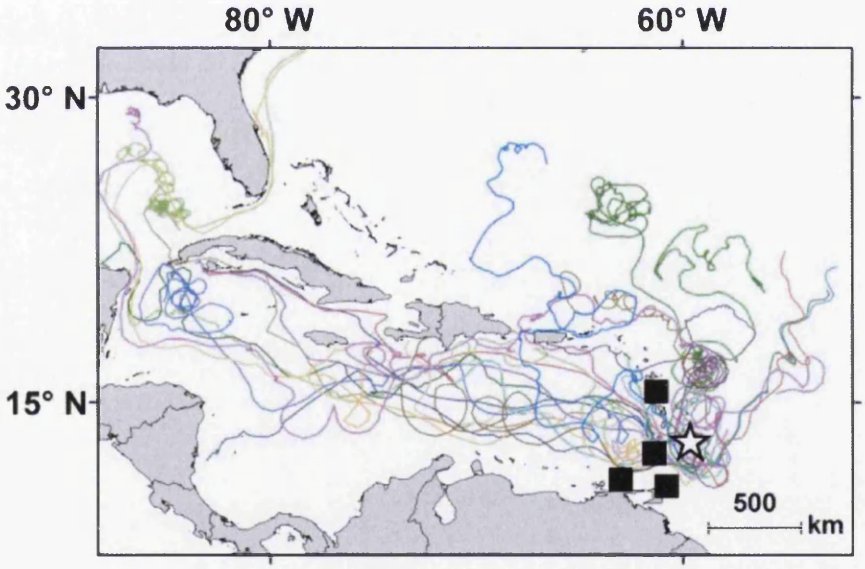

Fig. S2d. Hawksbill turtles (n=4) tracked from Barbados (Horrocks *et al.* 2001) Drifters travelled broadly west and north past the Windward Caribbean Islands and into the North Atlantic or west and south towards the Windward Caribbean Islands and then into the Caribbean sea. All turtles migrated from Barbados (the most Eastern Windward Island), to other Windward Islands (c.200-400 km) to the north, west and south of Barbados. Symbols follow those detailed in Fig. S2a.

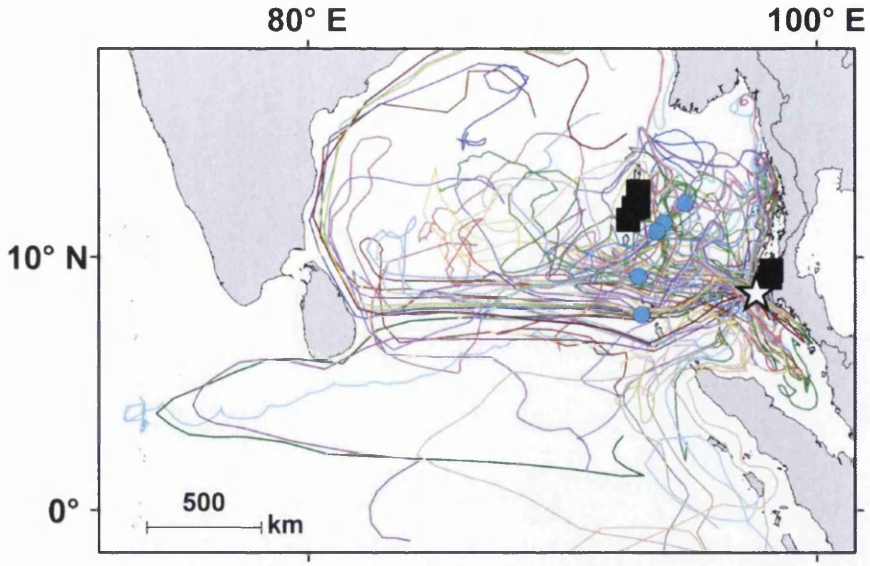

Fig. S2e. Green turtles (n=7) tracked from Huyong Island, Thailand (Yasuda *et al.* 2006). Turtles travelled along a subset of a broad range of potential drift routes, five green turtles migrated broadly west and NW to foraging habitats in the Indian Andaman Islands, whilst two migrated much shorter distances to a nearby Island off the coast of mainland Thailand. Drifters dispersed broadly throughout the Andaman Sea, Bay of Bengal and south into the Indian Ocean. Symbols follow those detailed in Fig. S2a.

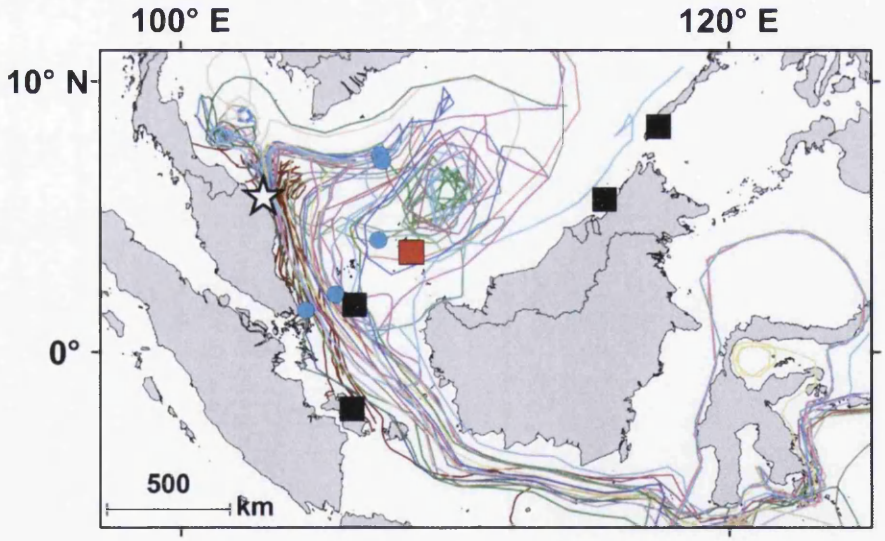

Fig. S2f. Green turtles (n=5) tracked from Redang Island, Malaysia (Papi *et al.* 1995; Luschi *et al.* 1996) Turtles travelled to their foraging habitats along broadly easterly-southerly trajectories. The tag transmissions stopped for one turtle in a location c. 600 km SE of the natal area before it reached its foraging habit (red square). Drifters spread along broadly easterly-southerly trajectories in accordance with the movements of turtles. Symbols follow those detailed in Fig. S2a.

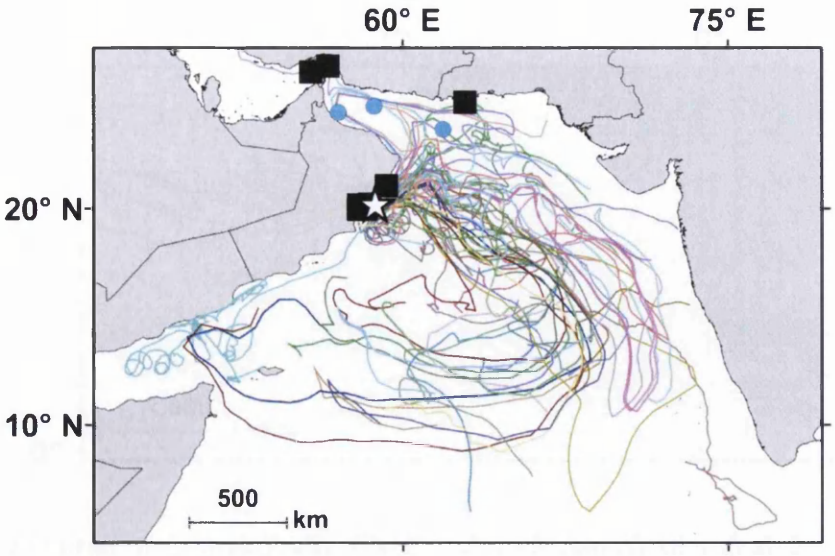

Fig. S2g. Olive ridleys (n=9) from Oman (Rees *et al.* 2012). Nine turtles migrated to discrete neritic foraging habitats, whilst one turtle performed pelagic wandering movements (more akin to leatherback turtles). Drifters dispersed broadly throughout the Arabian Sea and into the Gulf of Oman. Most turtles foraged locally near their natal area, whilst the other three migrated along a subset of a wide range of potential drift trajectories. Symbols follow those detailed in Fig. S2a.

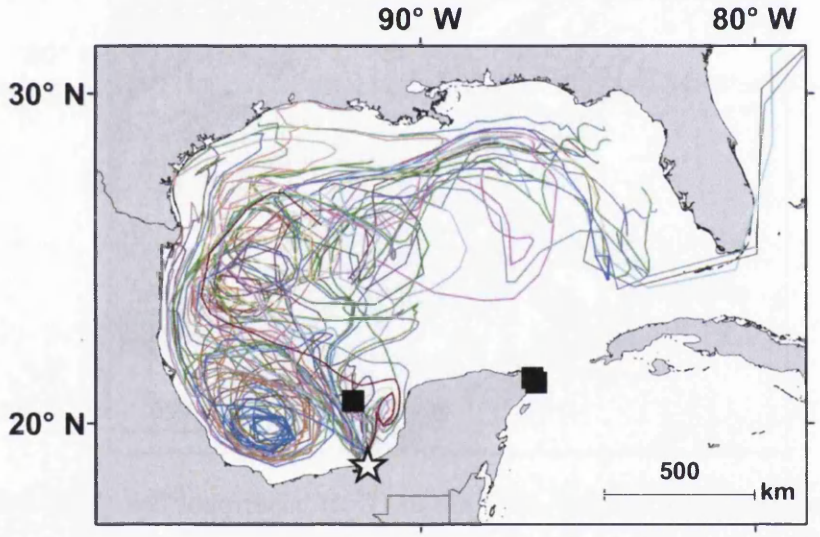

Fig. S2h. Hawksbill turtles (n=3) from Campeche, Mexico (Cuevas *et al.* 2008). One turtle foraged c. 100 km north of the natal area, whilst two turtles travelled along the coast broadly NE then east around the Yucatan Peninsula to their foraging habitats (c. 600 km away). Local retention of drifters was high, only 8% passed the east coast of Florida with the Gulf Stream, the rest remained within the Gulf of Mexico and hence turtles are anticipated to have encountered there foraging habitats within the Gulf of Mexico during their first few years of life. Symbols follow those detailed in Fig. S2a.

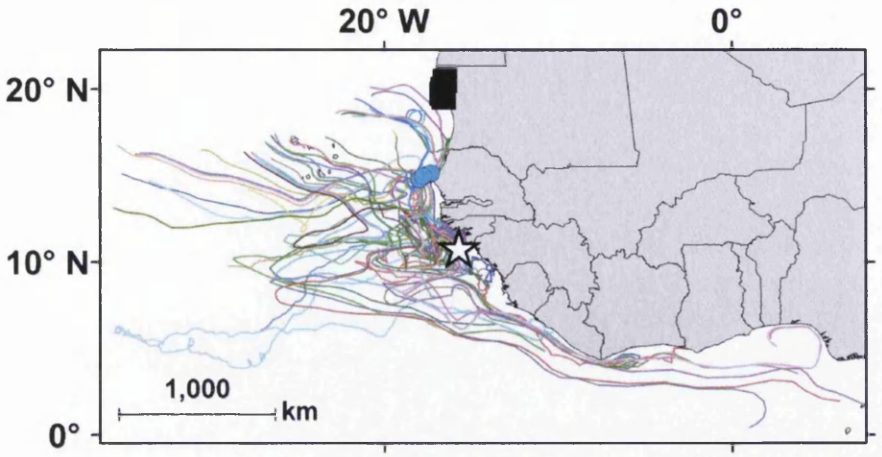

Fig. S3i. Green turtles (n=3) from Poilão Island, Guinea Bissau (Godley et al. 2010). Turtles all migrated north along the coast c. 1000 km to Mauritania. Drifters dispersed broadly north along the coast towards Mauritania or south along the coast of Africa, or towards the Cape Verde Islands/into the North Atlantic Gyre. Symbols follow those detailed in Fig. S2a.

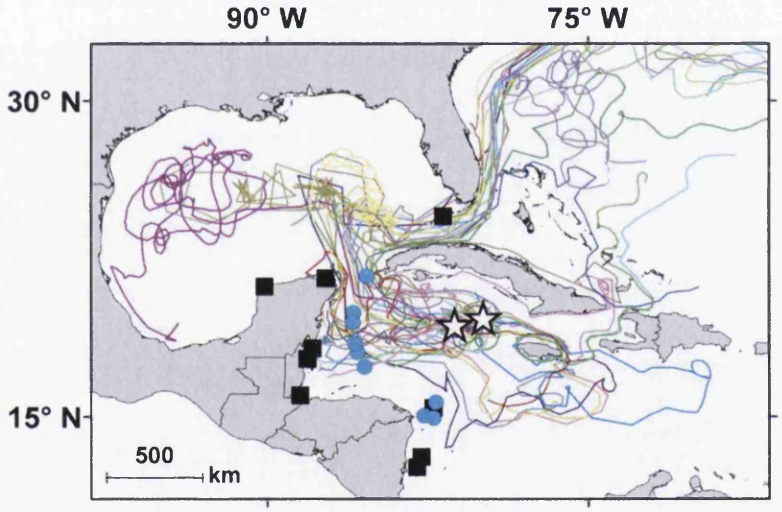

Fig. S2j. Green (n=7) and loggerhead (n=3) turtles from Cayman islands (Blumenthal *et al.* 2006) Turtles were tracked to a broad range of foraging habitats broadly south, west and north of the Cayman Islands. Drifters dispersed widely throughout this area, with c.89 % of drifters initially travelling broadly west and south, 82% of drifters then passed the east coast of Florida in the Gulf Stream Turtles migrated to a subset of a range of sites they could have encountered. Symbols follow those detailed in Fig. S2a.

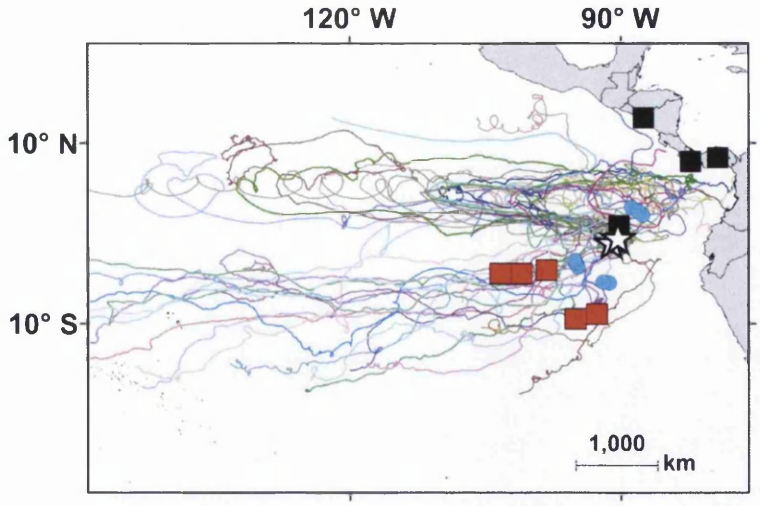

Fig. S2k. Green turtles (n=10) from the Galapagos Islands (Seminoff *et al.* 2008). Three turtles migrated NW to neritic foraging habitats in central America, two turtles remained resident in the Galapagos. Fiver turtles migrate SE however tag transmissions stopped in oceanic areas (red squares) before turtles were confirmed to have reached their foraging locations. Seminoff *et al.* (2008) have suggested these turtles are oceanic foragers (although the early failure of tags could not confirm this). Drifters dispersed broadly north towards central America and west or broadly south and west. The nearest substantial land mass (the French Polynesia islands) along the south westerly trajectories lie > 5000 km from the natal area. Symbols follow those detailed in Fig. S2a.

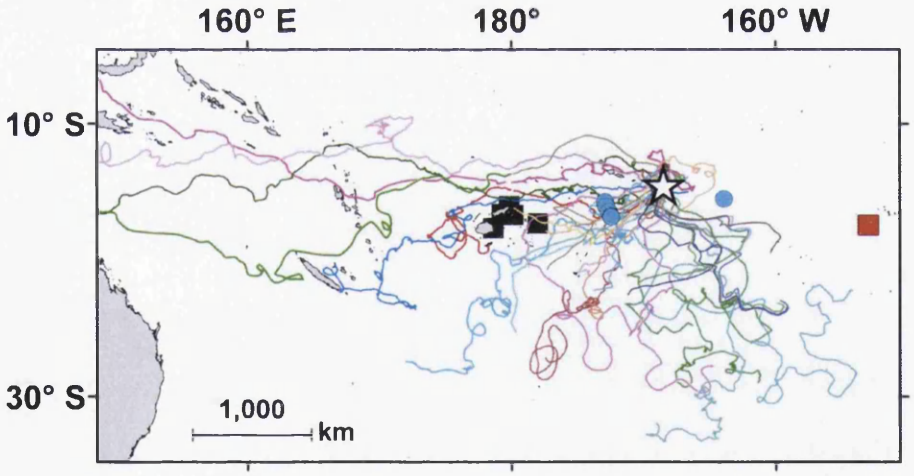

Fig. S2l. Green turtles (n=7) from America Samoa (Craig *et al.* 2004). Six turtles migrated broadly WSW towards Fiji (in agreement with the prevailing south and westerly ocean ccurrent flows). Five of these turtles reached their foraging grounds. The seventh turtle travelled broadly east towards French Polynesia; however transmissions stopped near (red square) before its foraging ground could be confirmed. Drift trajectories reveal that this turtle is likely to have encountered French Polynesia through a more convoluted drift trajectory as c. 20% of drifters started to drift in this direction. Symbols follow those detailed in Fig. S2a.

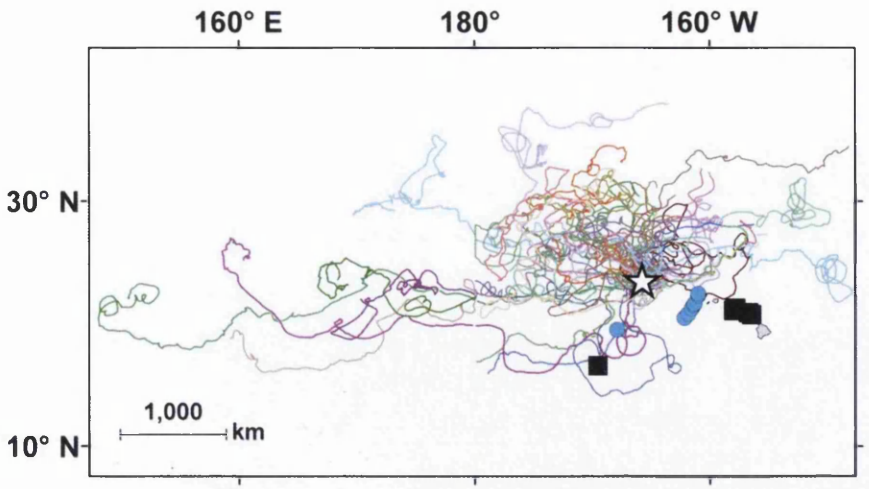

Fig. S2m. Green turtles (n=8) from the French Frigate Shoals (NW Hawaii) (Balazs 1994; Balazs *et al.* 1994; Balazs and Ellis 1998). Seven turtles migration SE towards the SW Hawaii islands, while one turtle migrated to a neritic area in Johnston Atoll. Local retention was high for some drifters due to high eddy activity, whilst others started to drift along trajectories that would lead to transoceanic movements in the North Pacific Gyre. Turtles migrated c.1000 km to the nearest land masses away from their natal rookeries that they would be expected to have encountered as hatchlings. Symbols follow those detailed in Fig. S2a.

Support for the second hatchling drift mechanism: Case 3

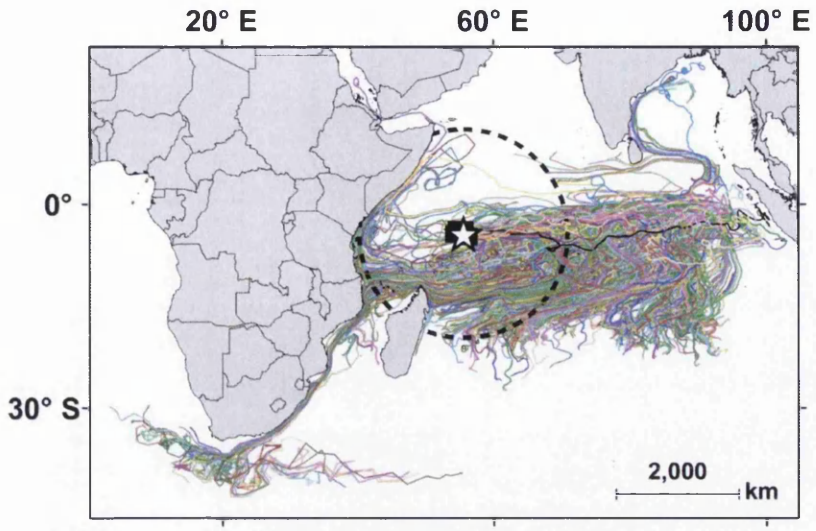

Fig. S3a. Hawksbills turtles (n=5) from Cousin Island, Seychelles (Mortimer and Balazs 2000). All turtles remained locally resident within the Seychelles Archipelago. The majority (> 80 %) of drifters travelled broadly east where they would not have encountered any other land mass for c.5000 km along this trajectory, drifters then travelled broadly south (in the Indian Ocean) or north (into the Bay of Bengal) or back west (towards Africa/Madagascar). A few drifters left the natal area and then travelled broadly west, then north/south towards Africa/Madagascar. These land masses lay within the 3000 km upper migration ceiling (dashed line; Hays and Scott in press) that post-nesting adult cheloniid turtles can travel to their foraging habitats. Coloured lines: all Lagrangian drift trajectories (> 1000) are plotted, dashed line: 3000 km buffer around the nesting sites. Other symbols follow those detailed in Fig. S2a.

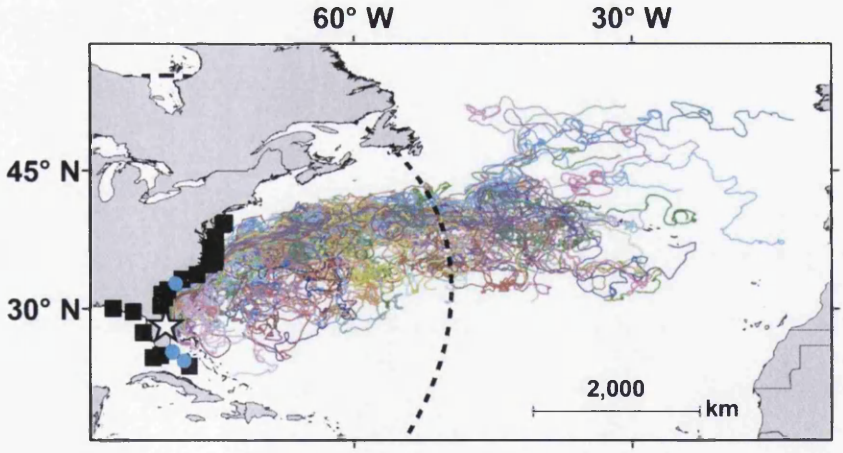

Fig. S3b. Loggerhead turtles (n=16) from Cape Canaveral, east Florida (Ardent *et al.* 2012). All turtles (bar one) migrated both north and south along the coast and around the Florida Panhandle and into the Gulf of Mexico. One turtle crossed open water to reach its foraging location in the Bahamas. Drifters tended to dispersed north, then east in the North Atlantic Gyre. The nearest landmass along this easterly drift trajectory is > 5000 km away and hence too

far for adult cheloniid turtles to return. Some drifters did not reach the eastern Atlantic and were entrained in eddies offshore from the mainland USA. Most notably, some of these drifters passed near the Bahamas (the only other land mass within 3000 km that drifters encountered) and also where the only turtle that left the mainland USA migrated. Symbols follow those detailed in Fig. S2a and Fig. S3a.

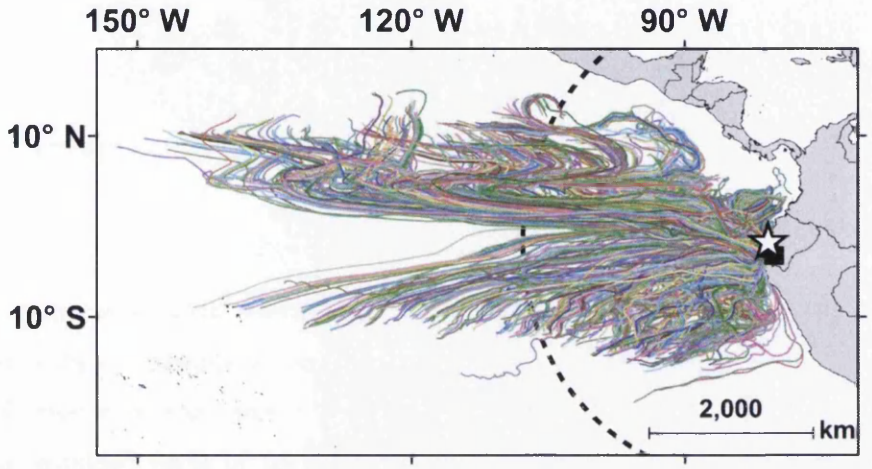

Fig. S3c. Hawksbill turtles (n=3) from Ecuador (Gaos *et al.* 2012). Turtles migrate short distances (c. < 200km) along the coast. Drifters disperse broadly north and then west or south and then west, not encountering any land mass away from the mainland, that an adult turtle could migrate to. Symbols follow those detailed in Fig. S2a and Fig S3a.

Case 4: Leatherback turtles

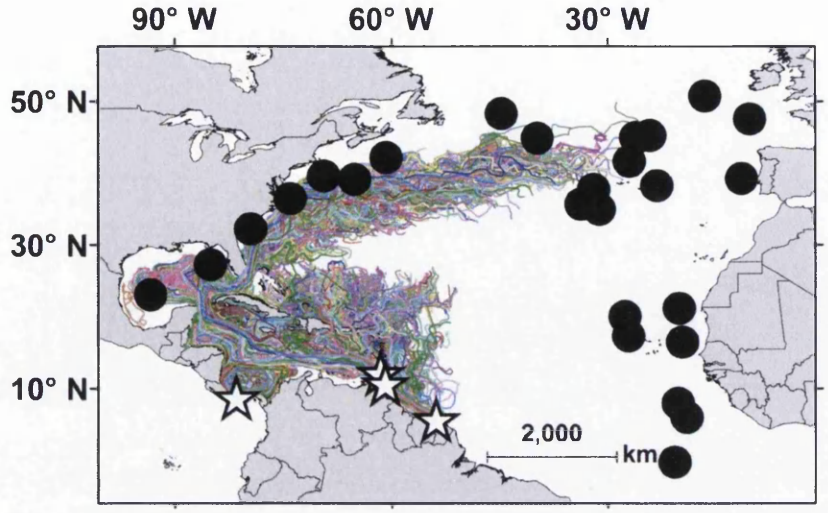

Fig. S4a. Leatherback turtles tracked from the French Guinea/Suriname Nesting complex, Trinidad, Grenada and Panama (Ferraroli *et al.* 2004; Eckert 2006; Hays *et al.* 2006; Fossette *et al.* 2010). Turtles dispersed widley throughout the North Atlantic, Carribean sea and Gulf of Mexico and remained north of the Equator. In one year, Lagrangian drifters also started to disperse widely throughout this area. All Lagrangian drift trajectories (> 1000) at each site are plotted. Black circles correspond to the location of leatherback tracks at their furthest from their natal area (indiciated by stars).

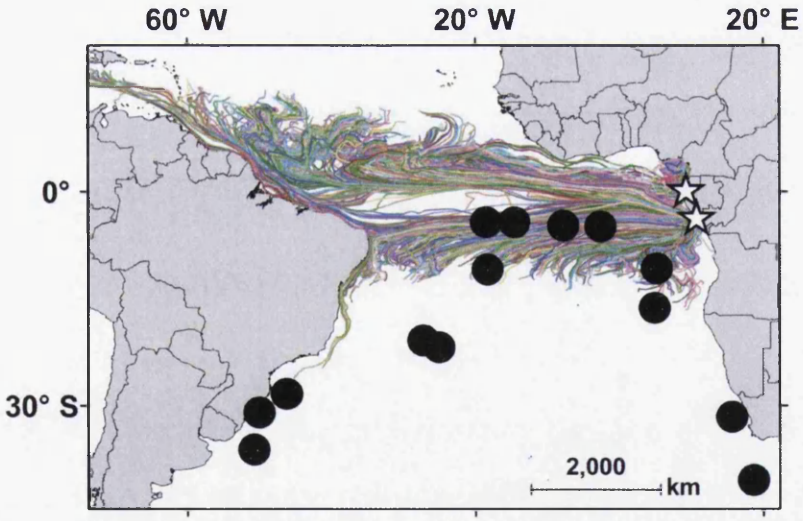

Fig. S4b. Leatherback turtles tracked from nestings beaches in the north and south of Gabon (Fossette *et al.* 2010; Witt *et al.* 2011) Turtles dispersed widely throughout the South Atlantic remaining south of the Equator. However, it is noteworthy that due to the bifurcation in the westward flowing South Equatorial current, all drifters from the northern nesting site drifted along the northern leg of the bifurcation towards the North Atlantic, whilst 86% of drifters from the southern nesting site drifted along the southern leg and disperse throughout the South Atlantic. Symbols follow those detailed in Fig. S4a.

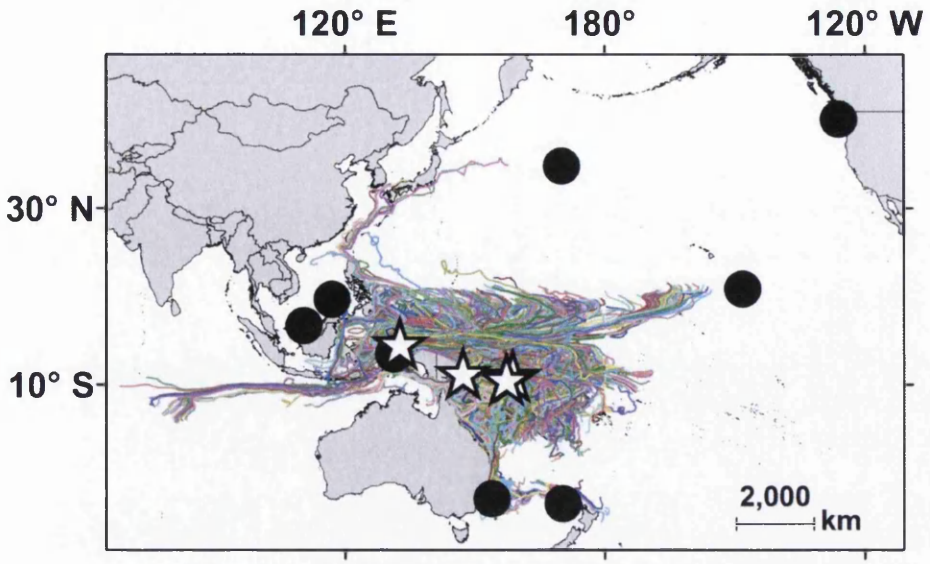

Fig. S4c. High use areas of leatherback turtles from nesting sites in Papua New Guinea, Indonesia, and the Solomon Islands (Benson *et al.* 2011). Turtles travelled widely throughout the Pacific, with some turtles foraging c. 11,000 km from their natal area. Symbols follow those detailed in Fig. S4a, however black circles correspond to high use areas of multiple individuals.

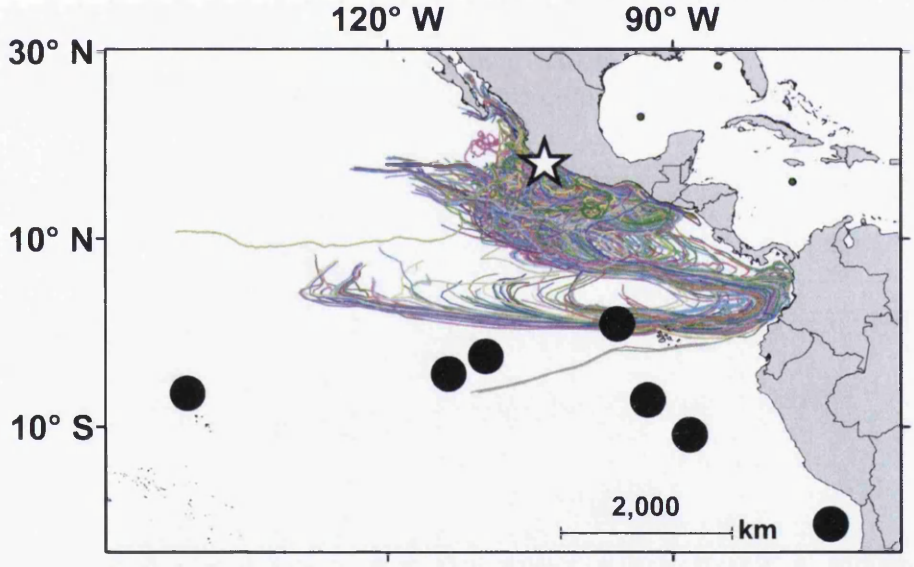

Fig. S4d. Leatherback turtles tracked from Mexiquillo, Mexico (Eckert 1997). Turtles travelled widely, all crossing the equator and into the South Pacific Ocean, it is noteworthy however that current flows captured by Lagrangian drifters tended to remain North of the equator. Symbols follow those detailed in Fig. S4a

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Epilogue

This thesis highlights a range of innovative ways in which Lagrangian analysis of animal movements and ocean current flows can be used to address key knowledge gaps in the life histories of marine organisms. Initially, by studying ocean current flows (and thus the cryptic hatchling dispersal phase) in the North Atlantic, the first robust estimates of the free living growth rates of hatchlings were obtained and by so doing, the long maturation times of turtle species highlighted (Chapter 1). Later, by programming small amounts of swimming behaviour of hatchlings into ocean model simulations, the ability of a small organism to influence its dispersal/survival chances in strong current flows was revealed (Chapters 2 and 3). Then, genetic analyses of stranded juvenile turtles combined with analysis into the pathways of ocean current flows and storm events revealed the role large storms can play in displacing hatchlings along aberrant routes (Chapter 4). Subsequent analyses of animal movement data revealed (1) an upper ceiling on the distance adult hard-shelled turtles can travel between nesting and foraging sites (Chapter 5) and (2) the importance of evidence based approaches for assessing the spatio-temporal effectiveness of MPA legislation for protecting sea turtles and their habitats (Chapter 6). Finally, research culminated in a global synthesis of the movement patterns of adult and hatchling sea turtles which provided global support for a new migration paradigm, that whilst adult turtles travel independently of ocean currents, ocean currents still indirectly drive the ontogeny of adult sea turtle migrations and foraging habitat selections due to their past experiences as drifting hatchlings (Chapter 7). The importance of studying hatchling dispersal thus extends, beyond the direct implications for the early life history stages, to implications for turtles throughout adulthood. The conservation of marine species has long been my primary interest/passion, and it is hoped that the findings and interdisciplinary and meta-analytical approaches presented in this thesis will be (1) used to inform conservation efforts and (2) further refined by others with emerging sea turtle/oceanographic datasets and other technological innovations.

The behaviour of hatchlings during the oceanic dispersal phase remains one of the least understood aspects of sea turtle life histories. Aside from loggerhead sea turtle populations in the SE US, there is a dearth of information on the hatchling swimming behaviour of other species and population. The best empirical datasets on the swimming

behaviour of loggerhead turtles from the SE US were derived from laboratory studies of neonate hatchlings (just a few days old). Consequently, the extent to which any swimming behaviours (e.g. directional swimming responses) changes with the ontogeny of hatchlings and the point when turtles can no longer be considered passive drifters remains enigmatic. Future innovations, e.g. through the continued efforts to miniaturise biotelemetry devices, are likely to prove instrumental in addressing some of these knowledge gaps and refining dispersal simulations for hatchling sea turtles and other marine organisms. Furthermore, research into hatchling dispersal to date, has been based on justifiable assumptions that the movement patterns of passively drifting hatchlings will reflect the movement patterns detailed through surface drifter buoys and ocean model simulations. Nonetheless, wind effects the movement pathways of surface drifters through both the forces exerted on the surface layer of the ocean and through the forces exerted on the drifter itself. The movement pathways of drifters are thus influenced by their physical properties (e.g. shape, size, mass, buoyancy and above sea surface projection). Whilst the impacts extreme atmospheric conditions in the form of large storms/hurricanes can have on hatchling dispersal were highlighted in my PhD, it is hoped that the extent to which less extreme and more regular storms/strong winds can influence the movement trajectories of surface drifters such as hatchlings can also be established.

As the spatio-temporal resolution and accuracy of ocean models continues to improve, so too, will our ability to more realistically model the dispersal of marine organisms. Nonetheless, the advent of higher resolution global ocean models is not anticipated to affect the broad-scale patterns in modelled hatchling dispersal; on which my PhD findings were based. For example, whilst investigating hatchling dispersal from seven nesting regions in the SE USA, the same broad-scale patterns in offshore movements were obtained by using two ocean models (a higher resolution 0.08 degree model and a lower resolution 0.25 degree model) and surface drifter buoys. The higher resolution model did however capture a greater retention of modelled drifters in coastal waters than the lower resolution model. However, since any hatchling sea turtles that remain in coastal waters are likely to very quickly succumb to predation, my research areas (and findings) were based on the movements of hatchlings that survived beyond the coastal zone and dispersed with offshore currents. Nonetheless, model resolution is an important consideration, particularly when fine-scale and higher energy oceanic

processes (such as small eddies) need to be accurately resolved or when research interest lie more heavily with coastal processes (fronts etc) and the dispersal of organisms in the coastal realm. In these instances however, it is anticipated that the coupling of the highest resolution (tide resolving) local coastal models with global offshore ocean circulation models will be key to gaining accurate descriptions of the dispersal pathways of organisms.